7-1-2015

Macroecology and Sociobiology of Humans and other Mammals

Joseph Robert Burger

Recommended Citation

Burger, Joseph Robert. "Macroecology and Sociobiology of Humans and other Mammals." (2015). https://digitalrepository.unm.edu/biol_etds/11

Joseph Robert Burger
Candidate

Biology
Department

This dissertation is approved, and it is acceptable in quality and form for publication:

Approved by the Dissertation Committee:

James H. Brown, Ph.D., Chairperson

Felisa A. Smith Ph.D., Co-Chairperson

Melanie E. Moses, Ph.D.

Bruce T. Milne, Ph.D.

MACROECOLOGY AND SOCIOBIOLOGY OF HUMANS AND OTHER MAMMALS

By
Joseph R Burger

B.A. Economics and International Studies, Francis Marion University 2006
M.S. Biology, University of Louisiana at Monroe 2010

DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of

Doctor of Philosophy
Biology

The University of New Mexico
Albuquerque, New Mexico

July 2015

DEDICATION

To my family: Mom, Dad, Ryan, Lily Ann, and Rachel. For always supporting me in all of my adventures in life, big and small.

ACKNOWLEDGEMENTS

I am tremendously grateful for the mentorship of my Ph.D. advisor, James H. Brown, for his thoughtful comments, criticisms, and inspiring discussions. My interactions with Jim have fundamentally changed how I approach science. I am also very thankful to my committee members Melanie Moses, Felisa Smith, Bruce Milne and honorary member, Randy Thornhill, for helpful feedback, guidance, and stimulating discussions during my time at UNM. I wish to thank many colleagues for their many discussions during my Ph.D. and especially the following whom I have had the pleasure of collaborating with: Craig Allen, Meghan Balk, Jim Brown, Bill Burnside, Mike Chang, John Day, Ana Davidson, Luis Ebensperger, Trevor Fristoe, Loren Hayes, Marcus Hamilton, Sean Hammond, Astrid Kodric-Brown, Christine Maher, Pablo Marquet, Norman Mercado-Silva, Matt Moerschbaecher, Adeline Murthy, Jeff Nekola, Jordan Okie, Tatiana Paz, Eric Roy, Tina Wey, Vanessa Weinberger, and Wenyun Zuo. I also thank my early mentors at Francis Marion University for encouraging an economics major to also explore natural history and my masters advisor, Loren Hayes, for accepting an economics major into his behavioral ecology lab. You have all influenced me greatly and I am forever thankful.

I am also thankful for financial and intellectual support from the following: the Program in Interdisciplinary Biological and Biomedical Science at the University of New Mexico; The Tinker Foundation and the Latin American and Iberian Institute; The American Society of Mammalogists; The Santa Fe Institute; a Joseph Gaudin Scholarship from UNM Biology.

And finally, a big thanks to the UNM Biology Department, the Program in Interdisciplinary Biological and Biomedical Sciences, and the Human Macroecology group for providing such a stimulating environment and the Ebensperger and Marquet labs at Pontificia Universidad Catolica de Chile for their hospitality and providing me a home away from home during extensive periods of my graduate work.

MACROECOLOGY AND SOCIOBIOLOGY OF HUMANS AND OTHER MAMMALS

By
Joseph R Burger

B.A. Economics and International Studies, Francis Marion University 2006
M.S. Biology, University of Louisiana at Monroe 2010
Ph.D. Biology, University of New Mexico 2015

ABSTRACT

Despite being the most studied species on the planet, ecologists typically do not study humans the same way we study other organisms. My Ph.D. thesis contributes to scientific development in two ways: i) synthesizing our understand of the inter and intraspecific variation in social behavior in an understudied rodent lineage, the caviomorphs, providing a comparative context to understand social evolution in general, and 2) developing a macroecological approach to understand the metabolic trajectory of the human species. Through comparative analysis, chapter 2 synthesizes the available information on the diversity of sociality in the caviomorph rodents, both within and across species. Studies and theory derived from better-studied mammalian taxa establish an integrative and comparative framework from which to examine social systems in caviomorphs. We synthesize the literature to evaluate variation in space use, group size, mating systems, and parental care strategies in caviomorphs in the context of current hypotheses. We highlight unique aspects of caviomorph biology and offer potentially fruitful lines for future research both at the inter and intraspecific levels. We can gain unique insights into the ecological drivers and evolutionary significance of diverse animal societies by studying this diverse taxon. Chapter 3 outlines core ecological principles that should be integral to a science of sustainability: 1) physical conservation laws govern the flows of energy and materials between human systems

and the environment, 2) smaller systems are connected by these flows to larger systems in which they are embedded, 3) global constraints ultimately limit flows at smaller scales. Over the past few decades, decreasing per-capita rates of consumption of petroleum, phosphate, agricultural land, fresh water, fish, and wood indicate that the growing human population has surpassed the capacity of the Earth to supply enough of these essential resources to sustain even the current population and level of socioeconomic development. Chapter 4 applies a socio-metabolic perspective of the urban transition coupled with empirical examination of cross-country data spanning decades. It highlights the central role of extra-metabolic energy in global urbanization and the coinciding transition from resource extraction to industrial and service economies. The global urban transition from resource producers in rural areas, to industrial and service employment in urban systems is fuelled by supplementing extra-metabolic energy in the form of fossil fuels for decreasing human and animal labor. Collectively, I hope this work demonstrates the utility of comparative analysis and synthesis in understanding the evolutionary ecology of sociality and the power of a macroecological approach in understanding the metabolic ecology and trajectory of the human species.

Table of Contents

List of Figures

List of Tables

CHAPTER 1: INTRODUCTION

Despite being the most studied species on the planet, ecologists typically do not study humans the way we study all other species. In 1975, E.O. Wilson published *Sociobiology* – the systematic study on the evolution of animal societies. Only the last Chapter of 27 dealt explicitly with humans, however, it generated one of the greatest controversies in modern science (Segerstrale 2001). How are the tools of science deployed appropriately to understand the ecology, evolution, and behavior of our own species? Wilson’s attempt to unify the sciences and provide an objective, evolutionary lens to view human behaviors was met with great resistance from a diverse intellectual community, including evolutionary biologists.

Twenty-five years later we entered the “century of complexity” (Hawking 2000) — where currencies of energy and information interpreted from first principles provides new macroecological approaches to understand the universal features of physical, biological, and social systems across all spatial and temporal scales. The emergence of such unifying and transdisciplinary science is exciting and timely given the unprecedented size of the human population, economy, and impact on the plant and the rest of species. Compilation and analysis of ‘big-data’ and simple, yet general mathematical theory, allows us to begin to explore empirically and model mathematically the universal constraints and emergent behaviors of physical, biological and social systems, including the emergence of the modern socioeconomic enterprise.

A necessary first step to unraveling broad-scale pattern and process in biological and social systems is to observe, quantify, and synthesize basic biological traits — the natural history — of organisms. Chapter 2 explores the diversity of social systems in the caviomorph rodent lineage. These rodents exhibit diverse social organization, reflecting the diverse ecological niches that they occupy. Studies and theory derived from better-studied taxa establish an integrative and comparative framework from which to examine social systems in caviomorphs. We synthesize the literature to evaluate variation in space use, group size, mating systems, and parental care strategies in caviomorphs in the context of current hypotheses. Across species, ecological lifestyles, including diet, habitat mode, space use, and activity period, are linked to variation in social systems including mating systems, breeding strategies, and associated parental care strategies. Within species, different populations and the same populations over time vary in space use, sociality, and mating systems, with most variation explained by differences in resource distribution, predation risk, or population density. We highlight unique aspects of caviomorph biology and offer potentially fruitful lines for future research both at the inter and intraspecific levels. Among species, better-resolved phylogenies and collation of basic natural history information including lifestyle characteristics, especially for underrepresented families such as spiny rats (Echimyidae) and porcupines (Erethizontidae), can advance comparative studies. Within species, future studies of caviomorphs can make use of recent technological advancements in data collection (e.g., proximity data loggers) and data analysis (e.g., model selection), as well as integration of laboratory and field studies. These complimentary approaches will allow us to examine the diversity of social behavior in this rich taxon at multiple levels of analysis. In doing so, we can gain unique insights into the ecological drivers and evolutionary significance of diverse social systems.

Chapter 3 outlines three ecological principles that govern all life on the planet, including modern humans. Yet sustainability science has developed largely independent from and with little reference to key ecological principles that apply to the human species. A macroecological perspective highlights three principles that should be integral to sustainability science: 1) physical conservation laws govern the flows of energy and materials between human systems and the environment, 2) smaller systems are connected by these flows to larger systems in which they are embedded, 3) global constraints ultimately limit flows at smaller scales. Over the past few decades, decreasing per-capita rates of consumption of petroleum, phosphate, agricultural land, fresh water, fish, and wood indicate that the growing human population has surpassed the capacity of the Earth to supply enough of these essential resources to sustain even the current population and level of socioeconomic development.

Chapter four investigates the macroscopic consequences of the global urban transition where more people now live in cities than rural areas. We analyze cross-country data spanning several decades from the World Bank to elucidate the patterns and processes that integrate biophysical and socioeconomic systems with urbanization. These include changes in per capita energy use and CO_2 emissions, shifts in resource and non-resource employment, and economic growth. Our analyses reveal that across nations and within nations over time, per capita Gross Domestic Product (GDP), energy use, and CO_2 production are lowest in predominantly rural countries (rural > urban pop.), increase most steeply across the urban transition (urban ≈ rural pop.) and are highest in the most urban countries (urban > rural pop.). These trends coincide with changes in employment by sector and gender. Rural economies are largely based on male employment in the primary resource-extraction sector, including agriculture, fisheries, and forestry. Urbanizing nations have predominantly male employment in the increasing industry sector, including public utilities. The most urban nations are dominated by service economies, with some countries having up to 90% of female employment in the service sector. The pervasive trend in employment across the rural-to-urban gradient was a decline in the proportion of the population employed in resource sectors and increase in the proportion working in non-resource (i.e., industrial and service) sectors.

These trends that accompany urbanization are likely due to two primary factors as economies transition from rural to urban: i) metabolic energy expended on human and animal labor is increasingly supplemented by extra-metabolic fossil fuel energy to power machines for extracting and transporting raw materials and to support industrial, technological, informational, and service economies in cities, and ii) energy is used to build and maintain the infrastructure that sustains flows of energy, materials, and information within, into, and out of urban systems. Increasing scarcity of energy and material resources, especially fossil fuels, poses formidable challenges for an urbanizing planet.

CHAPTER 2: DIVERSITY OF SOCIAL BEHAVIOR IN CAVIOMORPH RODENTS

Forthcoming as: Maher, CR, JR Burger. Diversity of social behavior in caviomorph rodents. – in press – in Sociobiology of caviomorph rodents: an integrative view. Ebensperger, LA & Hayes, LD. Eds. Wiley.

Key terms and definitions (source):

Aggregation: Groups in which individuals share a common space (Ebensperger & Hayes, this volume)

Allonursing: Individuals nurse from female other than their mother (Hayes, L. D. 2000. Animal Behaviour 59:677-688).

Alloparental care: Care provided to nondescendant offspring by breeders or nonbreeders (Ebensperger & Hayes, this volume)

Altricial: Neonates born in a relatively undeveloped condition (eyes closed, minimal fur present) and require prolonged parental care (Feldhamer et al. 2004)

Altruism: Helpful behavior that raises the recipient's direct fitness while lowering the donor's direct fitness (Alcock, J. 2013. Animal behavior: an evolutionary approach. 10th ed. Sinauer Associates Inc., Sunderland, Massachusetts.)

Breeding strategy: Form of cooperation that describes the degree to which direct reproduction and parental effort is shared (reproductive skew) within groups (Ebensperger & Hayes, this volume)

Dominance hierarchy: Association ranks that in social species result from agonistic interactions and determine access to critical resources and breeding (Ebensperger & Hayes, this volume)

Eusociality: Colonies contain specialized nonreproductive castes that work for the reproductive members of the group (Alcock, J. 2013. Animal behavior: an evolutionary approach. 10th ed. Sinauer Associates Inc., Sunderland, Massachusetts.)

Female defense polygyny: Mating system in which a male fertilizes the eggs of several partners in a breeding season and in which the male directly defends several mates (Alcock, J. 2013. Animal behavior: an evolutionary approach. 10th ed. Sinauer Associates Inc., Sunderland, Massachusetts.)

Inclusive fitness: The sum of an individual's direct and indirect fitness (Alcock, J. 2013. Animal behavior: an evolutionary approach. 10th ed. Sinauer Associates Inc., Sunderland, Massachusetts.)

Mating system: Association between males and females during breeding activity, including number of sexual partners that an individual has and the parental care strategies of males and females (Ebensperger & Hayes, this volume)

Parental care: Extent to which male and female parents provide care to their offspring (Ebensperger & Hayes, this volume)

Plural breeding: Breeding strategy in which most females (and males) in the same social group breed (i.e., exhibit low reproductive skew; Ebensperger & Hayes, this volume)

Precocial: Born in a relatively well developed condition (eyes open, fully furred, and able to move immediately) and requiring minimal parental care (Feldhamer et al. 2004)

Reciprocity: A helpful action is repaid later by the recipient of the assistance (Alcock, J. 2013. Animal behavior: an evolutionary approach. 10th ed. Sinauer Associates Inc., Sunderland, Massachusetts.)

Reproductive skew: Degree to which certain members of a group are prevented from breeding

Resource defense polygyny: Mating system in which a male fertilizes the eggs of several partners in a breeding season and in which the male acquires several mates attracted to resources under the males' control (Alcock, J. 2013. Animal behavior: an evolutionary approach. 10th ed. Sinauer Associates Inc., Sunderland, Massachusetts.)

Social behavior: The entire array of behavioral interactions among members of the same species that result in fitness consequences for all individuals involved (Ebensperger & Hayes, this volume)

Social monogamy: One male pairs with one female

Social network: Finite set of actors and the relations among them (Wasserman, S. 1994. Social network analysis: methods and applications. Cambridge University Press.)

Social organization: Outcome of a consistent set of social relationships (Hinde, R. A. 1983. A conceptual framework. In: Primate social relationships (Hinde, R. A., ed.). Blackwell Scientific Publications, Oxford, United Kingdom, pp. 1-7.

Social system: Emergent outcome of a social relationship that seems to have a biological function (Lott 1991)

Sociality: Group living

Territoriality: Exclusion of conspecifics by single or groups of individuals from access to a portion of its (their) range (Ebensperger & Hayes, this volume)

Abstract

Caviomorphs occupy diverse ecological niches and exhibit diverse social organization. Studies and theory derived from better-studied mammalian taxa establish an integrative and comparative framework from which to examine social systems in caviomorphs. We synthesize the literature to evaluate variation in space use, group size, mating systems, and parental care strategies in caviomorphs in the context of current hypotheses. Across species, ecological lifestyles, including diet, habitat mode, space use, and activity period, are linked to variation in social systems including mating systems, breeding strategies, and associated parental care strategies. Within species, different populations and the same populations over time vary in space use, sociality, and mating systems, with most variation explained by differences in resource distribution, predation risk, or population density. We highlight unique aspects of caviomorph biology and offer potentially fruitful lines for future research both at the inter and intraspecific levels. Among species, better-resolved phylogenies and collation of basic natural history information including lifestyle characteristics, especially for underrepresented families such as spiny rats (Echimyidae) and porcupines (Erethizontidae), can advance comparative studies. Within species, future studies of caviomorphs can make use of recent technological advancements in data collection (e.g., proximity data loggers) and data analysis (e.g., model selection), as well as integration of laboratory and field studies. These complimentary approaches will allow us to examine the diversity of social behavior in this rich taxon at multiple levels of analysis. In doing so, we can gain unique insights into the ecological drivers and evolutionary significance of diverse social systems.

Key words: ecological lifestyles, intraspecific variation, mating systems, parental care, social system, space use

Introduction

Social organization in mammals varies remarkably from solitary living, where interactions occur only between males and females during mating and between mothers and offspring prior to independence, to complex societies involving reproductive division of labor. Within a species, individuals may vary in social organization, either temporally within the same population or spatially across populations (Lott 1991). Researchers have described such diversity in several taxa, including primates (Clutton-Brock 1974; Clutton-Brock & Harvey 1977; Kappeler & van Schaik 2002), ungulates (Jarman 1974), carnivores (Macdonald 1983; Bekoff et al. 1984; Gittleman 1989), macropodid marsupials (Fisher & Owens 2000), and cetaceans (Mann et al. 2002). However, compared to these groups, we have less information about diversity and patterns in social behavior of rodents, the most diverse order (> 40% of species) of mammals (Feldhamer et al. 2004). If we are to understand general patterns of social behavior and develop theory from which we can deduce mechanisms, we must better understand the sociobiology of rodents.

The sociobiology of some rodent lineages is relatively well studied, including sciurids (Michener 1983; Blumstein & Armitage 1998; Koprowski 1998; Hare & Murie 2007), arvicolines (Viitala et al. 1996; Getz et al. 2005), heteromyids (Randall 2007), and bathyergids (Faulkes & Bennett 2007). Nonetheless, other speciose taxa that span environmental gradients of habitat complexity and seasonal variation also show potential for diverse variation in social behavior. The New World hystricognath rodents (caviomorphs) offer unique opportunities to examine ultimate (evolutionary and adaptive) and proximate (developmental and physiological) factors associated with variation in social organization across and within species. Closely related, they nonetheless occupy a diverse range of habitats spanning lowland wet tropics to high dry deserts in the temperate zone, and habits ranging from arboreal to semi-aquatic to subterranean (Hayes & Ebensperger 2011). They include the largest rodents on Earth, past and present (Alexander 2003), and they feature life history traits (Ernest 2003) and molecular divergence that lead some researchers to question whether caviomorphs should even be considered rodents, or if they deserve an order of their own (Graur et al. 1991). Although research on this group has increased substantially in the past decade (e.g., Hayes et al. 2011), we still lack a general understanding and synthesis of the sociobiology of caviomorphs, including similarities and differences with other taxonomic groups.

Our goal in this chapter is to review variation in social systems both among and within species in the context of withstanding models of mammalian systems. Social systems emerge at the population level, reflecting the outcome of social relationships among individuals and serving a biological function (Lott 1991). Moreover, social behavior includes all types of interactions among conspecifics in various contexts, e.g., mating, care of offspring, space use, cooperation, and group living (Ebensperger & Hayes, this volume). Thus, individual social interactions result in specific social systems. Specifically, we examine the following questions. How do group size (i.e., sociality), space use, mating systems, and parental care fit into the contexts of current hypotheses to explain variation in caviomorph social systems? How does sociality of caviomorph rodents compare with other mammalian taxa? Are social systems in caviomorphs a result of convergence with other species due to similar ecological conditions, or are there strong phylogenetic constraints to social evolution?

We hope this review provides a foundation and framework for future studies to explore the diversity of social behavior among, across, and within different populations of caviomorph rodents, and between caviomorphs and other mammal lineages.

The comparative approach in sociobiology

Comparative studies seek to reveal the phylogenetic origins and broad-scale distribution of social variation and the processes that maintain them. This approach is particularly useful for testing ultimate hypotheses that cannot be subjected to experimental manipulation. By revealing associations between ecological lifestyles, phylogenetic conservatism, and variation in social systems, we can begin to understand how natural selection has provided the diversity of social behaviors among caviomorph rodents within evolutionary and ecological constraints.

Most hypotheses to explain interspecific variation in social systems of mammals work from the bottom-up, focusing on how variation in the physical environment drives patterns in resource availability. The temporal and spatial distribution of resources in turn determines the distribution and spacing of individuals in populations. A uniform distribution of resources typically results in a hyperdispersed population, which prevents individuals from securing access to large quantities of resources (Komers & Brotherton 1997). In contrast, patchily distributed resources result in aggregations of individuals allowing opportunities for males to defend those resources to which females require access (resource defense polygyny) or to defend groups of females that aggregate at resource patches (female defense polygyny) (Emlen & Oring 1977; Langbein & Thirgood 1989).

Uncertainty in the spatiotemporal environment ultimately may drive interspecific variation in sociality (Jetz & Rubenstein 2011; Rubenstein 2011). Such variation in resource availability influences the distribution and density of individuals within a population. The ecological constraints hypothesis (Emlen 1982) is generally used to understand the role of habitat or resource limitations on dispersal strategies. However, it also recognizes the importance of environmental uncertainty, both spatially and temporally, in influencing the evolution of cooperative behaviors (Rubenstein 2011). Thus, sociality is hypothesized to evolve where resource availability is less predictable and resources are clumped either temporally or spatially, resulting in clumped distributions of individuals. High local densities of individuals likely attract predators, which in turn results in a positive feedback of selection processes that reduce predation risk such as alarm calling (Blumstein & Armitage 1998), increased body size (Sibly & Brown 2007), and changes in socioecological lifestyle including burrow use (Ebensperger & Blumstein 2006). Among burrowing species, spatial heterogeneity in drainage and soil types may foster aggregation (Hare & Murie 2007). Burrowing species may additionally benefit from increased burrowing efficiency from digging chains (Ebensperger & Bozinovic 2000), further selecting for group living.

Interspecific comparisons of social systems in caviomorphs

Sociality in caviomorphs ranges from solitary living, in the case in most spiny rats (Echimyidae) and tuco-tucos (Ctenomyidae), to aggregations of more than 100 individuals in capybaras (*Hydrochoerus hydrochaeris*; Caviidae) and maras (*Dolichotis patagonum*; Caviidae). Two studies used quantitative comparative methods to investigate the evolution of sociality in caviomorphs and found that variation in sociality (i.e., group size) correlates positively with increasing body size, diurnal activity patterns, and burrowing lifestyles (Ebensperger & Cofré 2001; Ebensperger & Blumstein 2006). However, group size is not influenced by plant cover, which reflects predation risk, or time to first reproduction, a measure of extended parental care (Ebensperger & Blumstein 2006). More recently, a phylogenetic analysis of caviomorphs suggested that group living was gained and lost repeatedly, perhaps originating from an ancestral species that was flexible in social organization, and that the loss of sociality correlated with use of habitats containing high vegetative cover (Sobrero et al. 2014).

In this section, we go beyond these studies of sociality based on group size and previous reviews of mating systems (Adler 2011; Adrian & Sachser 2011) and focus on interspecific variation in three main components of social systems: (i) mating systems, (ii) breeding strategies (i.e., degree to which direct reproduction and parental effort are shared within groups), and (iii) corresponding offspring care strategies. First, we address three questions that highlight unique aspects of caviomorph sociobiology: (i) What is the taxonomic distribution of social systems and ecological lifestyles? (ii) What is the prevalence of male-female pairs? and (iii) What is the prevalence and distribution of plural breeding and alloparental care? Then we offer future directions for comparative studies of caviomorph social systems and highlight taxonomic groups that lack basic information on social systems. Our comparative assessment also reveals species and groups that exhibit unique characteristics that may prove fruitful if pursued within the context of current theory.

Ecological lifestyles and taxonomic distribution of social systems

Across caviomorphs, body size ranges an astounding three orders of magnitude, from the smallest spiny rats that weigh ~30 g to capybaras that measure ~50,000 g, the largest of all extant rodents (Fig. 2.1). The majority of caviomorphs are small-bodied and solitary, whereas sociality, cooperation in the form of plural breeding, and a mating system based on male-female pairs seem more common among a few, large-bodied species (Fig. 2.1).

Some families of caviomorphs exhibit high degrees of sociality, whereas others are predominately solitary. Of the 18 species of Caviidae (cavies, maras, and capybaras), 7 (38.9%) are known to be social. Six of 13 species (46.2%) of Dasyproctidae (agoutis and acouchis) are reportedly social. Sociality has been documented in the majority (4 of 6 species, 66.7%) of species in the Chinchillidae family and in the single extant member of Dinomyidae (pacarana, *Dinomys branickii*). In contrast, at least 4 of 13 species (30.8%) in the Octodontidae are social (degus, *Octodon degus*; cururos, *Spalacopus cyanus*; and mountain degus, *Octodontomys gliroides*; Rivera et al. 2014). Among the most diverse family of caviomorphs, Echimyidae, only two of 90 species (2.2%) are known to be social (Yonenaga's Atlantic spiny rats, *Trinomys yonenagae*, and Atlantic bamboo rats, *Kannabateomys amblyonyx*). Finally, each of the following families has only a few social species each: Cuniculidae (1 of 2 species), Abrocomidae (3 of 10 species), Myocastoridae (1 species), and Ctenomyidae (3–4 of 60 species). With the exception of the North American porcupine, *Erethizon dorsatum*, little is known of the social systems of New World porcupines (Erethizontidae, with 16 species). Our analysis does not include island hutias (Capromyidae), which are poorly studied and generally in decline.

Of the species known to be social, over half (13 of 22) live in burrows (Appendix 1). Of these, only colonial tuco-tucos (*Ctenomys sociabilis*) and cururos are small-bodied and subterranean. Two large-bodied social caviomorphs (capybaras and nutrias, *Myocastor coypus*) are semi-aquatic, and only one social species is arboreal (Atlantic bamboo rats). Nearly two-thirds (14 of 22) of social caviomorphs are diurnal with tropical Atlantic bamboo rats and agoutis and pacas of the family Dasyproctidae being notable nocturnal exceptions (Appendix 1).

Male-female pairs

Social monogamy, i.e., one male pairs with one female, is rare in mammals (< 10% of species; Lukas & Clutton-Brock 2013), and caviomorphs are no exception. Across caviomorphs, male-female pairs occur in 6% (10/157) of species with known mating systems (L. D. Hayes & J. R. Burger, unpublished data; Appendix 1). One hypothesis for the evolution of social monogamy highlights the benefits of paternal care, including caring for or provisioning of young (Woodroffe & Vincent 1994). Less than half (40%) of caviomorphs organized as male-female pairs display paternal care, which is similar to that observed across mammals (Lukas & Clutton-Brock 2013). Alternatively, male-female pairs without paternal care may arise from mate guarding when males are unable to monopolize multiple breeding opportunities due to low female densities, territoriality among females, or large or drifting home ranges as a result of low quality homogenous or dispersed resource distributions (Komers & Brotherton 1997).

Male-female pairs without paternal care is prevalent in large-bodied, frugivorous tropical species (e.g., agoutis and acouchies, pacarana, and pacas; Appendix 1). These animals do not actively burrow but rather use pre-existing burrows or cavities for shelter. They forage on large seeds and fruits that are seasonally available and spatially dispersed, resulting in low densities and nonoverlapping home ranges (Dubost 1988; Eisenberg 1989). These species may provide fruitful study systems to further evaluate the mate guarding-social monogamy hypothesis (Komers & Brotherton 1997; Lukas & Clutton-Brock 2013).

Atlantic bamboo rats are unique among caviomorphs in that they exhibit male-female pairs with biparental care (Silva et al. 2008). Bamboo rats of the genera *Kannabateomys* and *Dactylomys* are large-bodied, nocturnal or crepuscular, obligate bamboo specialists that exhibit similar ecological lifestyles (Adler 2011; J. R. Burger, personal observation). Bamboo is a low quality, patchily distributed resource, and pairs may be able to defend bamboo patches (Silva et al. 2008). Males of *Kannabateomys* and *Dactylomys* produce conspicuous staccato vocalizations, probably used to advertise territories (LaVal 1976; Dunnum & Salazar-Bravo 2004). Further investigation into their social systems may provide unique opportunities to gain insights into social monogamy with biparental care in caviomorphs.

The Patagonian mara (*D. patagonum*) is an exception to the mate-guarding hypothesis for social monogamy. Maras display a social system perhaps unique in mammals yet loosely comparable to gregarious birds. Multiple breeding pairs live colonially (Taber & Macdonald 1992). Males do not provide care to offspring directly but exhibit vigilance and antipredator protection of offspring and mates (Macdonald et al. 2007). Male maras also assist females in excavating den sites before parturition, although adults do not inhabit burrows (Taber & Macdonald 1992). Despite rearing pups collectively in warrens, mothers nurse their own young and deliberately avoid allonursing except in rare cases where orphaned pups are nursed (Taber & Macdonald 1992). These characteristics raise interesting questions about mechanisms of offspring recognition. Pups appear to recognize mothers by distinguishing their whistle from those of other females. Mothers and fathers also appear to recognize pups, as females assess pups by sniffing the rumps and flanks before allowing them to nurse (Taber & Macdonald 1992). Thus, maras provide a unique system to understand mechanisms of parent-offspring recognition and group living without confounding effects of inclusive fitness or reciprocity.

Group living and alloparental care

Among caviomorphs for which the social system is known, sociality coupled to plural breeding occurs in 11% (17/157) of species. Of the plural breeders, alloparental care has been documented in 65% (11/17) of species (Appendix 1). Of those, paternal care is found in all species except the southern mountain cavy, *Microcavia australis* (Tognelli et al. 2001). Of the species that exhibit alloparental care, degus are particularly interesting because multiple females breed simultaneously and nurse their own young while indiscriminately accepting and nursing pups from others (Becker et al. 2007; Ebensperger et al. 2007). These groups are sometimes composed of kin but also include nonkin (Ebensperger et al. 2004; Ebensperger et al. 2009; Quirici et al. 2011a). This unique social system lends itself well to studies of inclusive fitness, altruism, and group selection.

Intraspecific variation in social systems of caviomorphs

Proposed hypotheses to explain variable social systems within species use a cost-benefit approach, where benefits associated with a particular social system must exceed costs, measured in terms of fitness (Brown 1964). Variation in social systems may be adaptive, allowing individuals to maximize fitness in environments with dynamic spatial heterogeneity and temporal variability (e.g., Wey et al. 2013). However, some aspects of social systems, such as living in larger groups, may result in decreased fitness (Lacey 2004; Hayes et al. 2009). Three sets of hypotheses have been invoked most commonly to explain the adaptive significance of population variation in mammalian social systems: resource distributions, predation risk, and population density (Lott 1991).

Consistent with resource-based hypotheses for interspecific variation in sociality (e.g., Emlen & Oring 1977), intraspecific studies also consider the influence of resource distribution and abundance on individual space use and, consequently, social and mating systems (Emlen & Oring 1977; Macdonald 1983; Slobodchikoff 1984; Travis et al. 1995; Brashares & Arcese 2002; Johnson et al. 2002; Maher & Burger 2011). Resources must be spatially or temporally distributed in ways that can be monopolized economically, i.e., benefits of accessing the resource outweigh costs associated with defense (Brown 1964; Emlen & Oring 1977; Brashares & Arcese 2002). Resources also can influence group size, with spatially or temporally clumped distributions favoring larger groups (Macdonald 1983; Johnson et al. 2002).

Another set of hypotheses focuses on predation risk and its effects on sociality and space use (Ebensperger 2001; Chapter 7, this volume). In particular, group living offers antipredator benefits including dilution of per capita risk (Krause & Godin 1995), group defense (Alexander 1974), and enhanced predator detection (Hoogland 1981; Ebensperger & Wallem 2002). Furthermore, habitat type influences social systems through predation risk. Open habitats increase risk and favor larger groups and larger body size, whereas closed or more structured habitats may reduce risk and shift the cost-benefit ratio toward smaller body size and solitary living (Jarman 1974; Brashares & Arcese 2002).

A third set of hypotheses addresses the role of population density in determining social systems (Lott 1991; Lukas & Clutton-Brock 2013). Extreme densities, whether high or low, may render defense of resources overly costly and thus ineffective (Maher & Lott 2000). Population density also may influence sociality and mating systems, with higher density promoting larger groups and multiple mating opportunities (Stallings et al. 1994; Lucia et al. 2008; Silva et al. 2008). Resource availability often influences population density and therefore social systems (Lott 1991). So population density may not be independent of resources (Lukas & Clutton-Brock 2013). Nonetheless, we include population density here because authors often explicitly address population density as a correlate or determinant of social systems.

Like other mammalian lineages (e.g., sciurid rodents, bovids, cervids, primates, and carnivores; Lott 1991), caviomorphs exhibit spatial or temporal intraspecific variation in space use, and, consequently, group living and mating systems. Of 11 extant families, intraspecific variation has been reported in 7 families (64%), and within those families, the extent of variation ranges considerably: Caviidae (7 of 18 known species), Echimyidae (3 of 85 known species), Dasyproctidae (2 of 13 known species), Ctenomyidae (2 of 60 known species), Cuniculidae (1 of 2 described species), Octodontidae (1 of 13 described species), and Chinchillidae (1 of 7 described species). Such differences probably say more about the extent to which fieldwork has been done on these animals than about the animals themselves.

Space use

Researchers exploring variation in space use described temporal changes in space use, primarily home range size and overlap, in just 8 species of caviomorphs (Maher & Burger

2011; Appendix 2). The degree of territoriality may change depending on resource conditions, e.g., capybaras become less territorial during the dry season yet continue to maintain exclusive areas (Macdonald et al. 2007). However, unlike other vertebrate taxa (Lott 1991; Maher & Lott 2000), virtually no caviomorph species shift from one type of spacing system to another, e.g., from a dominance hierarchy to territoriality. Changes from one spacing system to another may occur in natural populations, but such changes may have gone undetected or unreported. The only study describing such change focused on captive guinea pigs (*Cavia porcellus*; Sachser 1986) and may result from artificial conditions not encountered in a natural setting.

The more common scenario is to observe shifts in size and location of home ranges in response to food availability, population density, or predation risk (Maher & Burger 2011; Appendix 2). In general, larger home ranges correlate with greater predation risk, whereas smaller home ranges correlate with greater food resources and increased population density (Maher & Burger 2011). However, many studies are limited in terms of the ability to draw definitive conclusions because they followed few individuals for only a short period. Certainly, types of habitat, body size, and the secretive nature of many caviomorphs present challenges to studies assessing possible changes in space use relative to ecological conditions.

Members of the family Ctenomyidae, the tuco-tucos, have been relatively well studied among caviomorphs, although most work has focused on just a few species (Pearson et al. 1968; Busch et al. 1989; Malizia 1998; Lacey & Wieczorek 2003; Cutrera et al. 2006; Tassino et al. 2011). Rio Negro tuco-tucos (*Ctenomys rionegrensis*) appear to vary in home range size and extent of overlap, with females occupying larger ranges and sharing more space in November versus May or September (Tassino et al. 2011). The authors did not describe changes in ecological conditions that could correlate with such changes in space use. Nonetheless, they suggested that increased overlap and size of home ranges could result from movements of juveniles that disturb females' home ranges and enable females to move between burrows (Tassino et al. 2011).

A little known echimyid, *Thrichomys apereoides*, exhibited changes in daily home range size and movements, as measured using the spool and line technique (de Almeida et al. 2013). Again, although the authors did not measure ecological conditions such as food abundance, and they did not report sample sizes for males and females or by season, they suggested that reproductive activity and lack of food during the dry season was associated with the smaller home ranges for females at that time (de Almeida et al. 2013). Although this explanation runs counter to resource-based hypotheses, *T. apereoides* may occupy smaller ranges to avoid predation during the dry season when movements on leaf litter may increase their vulnerability to predators (de Almeida et al. 2013). Conversely, a study of Central American agoutis (*Dasyprocta punctata*) included data on food density. As predicted by resource-based hypotheses, home range size decreased as food resources increased, measured as density of *Astrocaryum* fruits or trees (Emsens et al. 2013).

Capybaras show changes in group size as habitat dries and forces animals to congregate near remaining water holes, effectively increasing population density (Herrera et al. 2011; see also Quirici et al. 2010). However, group size (population density) had no effect on home range size (Corriale et al. 2013). Rather, home range sizes decreased in spring and summer when food became more abundant. Group sizes also did not vary much across groups (range of total group size = 25.8–35.6; range of number of adults = 14.3–18.4;

Corriale et al. 2013), and population density may not have varied sufficiently to affect individual space use.

Characteristics of home ranges in capybaras also vary spatially with some populations exhibiting greater amounts of home range overlap than others (Corriale et al. 2013). Indeed, territoriality is reported in one population in Venezuela where capybaras experience more extreme environmental conditions, i.e., less abundant food from ponds drying out completely (Herrera & Macdonald 1989). Under less stressful conditions capybaras may not maintain exclusive territories, although core areas did not overlap (Corriale et al. 2013), suggesting some degree of exclusive use.

Although few, if any, caviomorphs change spacing systems completely, several species show spatial and temporal variation in size and overlap of home ranges beyond male-female differences that are widespread among mammals. Ecological conditions that are reported or predicted to correlate with such changes in caviomorphs, including resources, predation risk, and population density, also are associated with variation in other mammalian taxa (Lott 1991; Maher & Lott 2000). We have no reason to suspect that ecological variables should affect space use in caviomorphs any differently from other mammalian taxa. Furthermore, some environments may not vary sufficiently in ecological conditions to cause shifts in space use. Nonetheless, the broad range of habitats that caviomorphs occupy, from wet tropics to seasonally arid environments, affords the opportunity to explore such variation further. In particular, it is important to determine why some taxa (e.g., cavids) seem more flexible than others.

Sociality

Six species of caviomorphs display temporal or spatial variation in sociality as measured by group size (Appendix 2). Our earlier review (Maher & Burger 2011) summarized the species in which group sizes are variable and linked to changes in ecological conditions. This variation is primarily due to variation in food abundance (pacas, *Cuniculus paca*; plains vizcachas, *Lagostomus maximus*; maras; and lesser cavies, *Microcavia australis*), but also water availability in capybaras and predation risk in degus due to differences in habitat structure.

Capybaras rely heavily on the availability of water for thermoregulation and to escape predators (Macdonald 1981). Water also has important effects on group size in this species. Two populations occupied the same habitat in the llanos of Venezuela, but water levels were controlled in one area through the use of dykes and other means compared to another area. The result was more predictable food and water resources in the more managed area, leading to larger groups that contained more females and more satellite males (Herrera 2013).

Food abundance may explain population differences in group structure in another cavy, *Galea musteloides*; however, the evidence for variation in sociality is inconclusive (Adrian & Sachser 2011). In Argentina, one dense population of 25 individuals occupied a stone wall, a somewhat artificial setting (Rood 1972). In a wild population, however, females did not overlap home ranges, whereas males overlapped with females and with other males (M. Asher, unpublished data cited in Adrian & Sachser 2011). In this species, groups may form in areas that can support them based on food abundance (Adrian & Sachser 2011).

Spatial and temporal variation in sociality of degus has been studied more extensively than in other caviomorphs. A comparison of two populations, one of which occupied a higher elevation site (equated with a more stressful environment due to colder temperatures), with more patchily distributed food and lower predation risk revealed differences in sociality (Ebensperger et al. 2012). Groups were smaller at the high elevation site, but only in one of two study years. In that year, predation risk was greater at the site with larger groups, food was more abundant but of lower quality, and soil was harder. However, food resources appeared to be less important than predation risk and burrowing costs (Ebensperger et al. 2012).

Comparing within the two populations, the only significant relationship between group size and ecological conditions was soil hardness and number of males in a group, but only for the low elevation population and only in one year (Ebensperger et al. 2012). The authors suggested that multiple factors influence sociality in this species. Although ecological differences could explain spatial variation in group size, the conditions they measured were less important influences on sociality within populations versus among populations (Ebensperger et al. 2012). However, the time scale of the study was relatively short (2 years) and number of groups relatively low (4–9, depending on population and year). Additional research, conducted over a longer time span that could allow conditions to fluctuate more widely, could yield more definitive answers about factors influencing sociality in this species.

On the contrary, mountain degus (*Octodontomys gliroides*) appear to be less variable (Rivera et al. 2014). Despite differences in abundance and distribution of food, predation risk, and soil hardness across two habitats, the two populations did not differ in group size or space use, as measured by home range overlap (Rivera et al. 2014). The authors suggest that past ecological conditions shaped sociality in the species, but mountain degus have not shifted their social system to reflect current conditions (Rivera et al. 2014).

A recent approach to describing social organization involves analysis of social networks, which reflect social relationships, including affiliation and conflict, among individuals (Wey et al. 2013). Among degu groups, social networks vary over time and by sex. Compared with males, females have more preferred associations during lactation, when communal nursing occurs within groups (Wey et al. 2013). Such changes are not linked to ecological conditions *per se* but rather reflect intersexual strategies. This is just one example of how social network analysis has the potential to improve our understanding of how relationships within groups change, often in subtle ways, as conditions change.

Mating systems

We know the least about intraspecific variation in mating systems in caviomorphs, perhaps because direct observations of behavior between individuals can be difficult in the field setting. Studies often rely on indirect evidence such as behavioral incompatibility or aggression in captive studies (Hohoff et al. 2002), DNA analysis (Zenuto et al. 1999a; Túnez et al. 2009), degree of sexual dimorphism (Cutrera et al. 2010), testis size (Zenuto et al. 1999b), or sizes and amount of home range overlap between sexes (Cutrera et al. 2010). Only three species (one cavid, *Cavia aperea*, and two echimyids, *Proechimys semispinosus* and *Kannabateomys amblyonyx*) have been reported to show differences in mating systems, switching from one system to another, and these changes are linked either to population density or to food distribution (Maher & Burger 2011; Appendix 2).

Coypus do not switch mating systems, but DNA evidence from two populations shows that they exhibit different degrees of polygyny. However, the authors did not discuss ecological differences that might explain those apparent behavioral differences (Túnez et al.

2009). Another species, Talas tuco-tuco (*C. talarum*), also differs in the extent of polygyny based on indirect evidence related to home range size and amount of sexual size dimorphism in two populations (Zenuto et al. 1999b; Cutrera et al. 2010). Although both populations are polygynous and sexually dimorphic, males formed dominance hierarchies at one site, Mar de Cobo, where they also occupied larger home ranges than females, which suggested stronger polygyny or greater monopolization of females by males (Cutrera et al. 2010). At the second site, Necochea, home range sizes did not differ between males and females, sexual size dimorphism was lower, and males did not form dominance hierarchies (Zenuto et al. 1999b; Cutrera et al. 2010). Furthermore, males at Mar de Cobo tended to be larger, suggesting a more polygynous system. Ecological conditions also varied in the two populations. Mar de Cobo was characterized by greater quantities of food and softer soils for burrowing, which could lead to females clustering in space and thus, enabling males to maintain access to multiple females more easily. In addition, population density was higher at Mar de Cobo, with sex ratios biased toward females, all of which could lead to a greater degree of polygyny (Zenuto et al. 1999b). The mating system of *C. talarum* therefore follows the pattern seen among other caviomorphs that vary in mating systems, with population density and food resources influencing the ability to monopolize mates. Nonetheless, the use of genetic tools to directly measure reproductive skew among males would prove helpful in these systems.

Summary and conclusions

Recent studies continue to highlight not only the diversity of social behavior in caviomorphs but also the social variation exhibited by some species. Unlike the majority of mammals, most caviomorphs are pair- or group-living, with sociality more prevalent in diurnal and larger-bodied species (Table 7.1, Chapter 7 of this volume). Similar to other mammals, few caviomorph species exhibit social monogamy, with paternal care rarely occurring. However, alloparental care and paternal care is widespread among plural breeding species. Within species, caviomorphs do not completely switch from one spacing system to another or from one mating system to another, whereas such switches occur in other mammalian taxa (Lott 1991; Maher & Lott 2000). Group size, however, fluctuates within some caviomorph species, as we see in other mammals (Lott 1991). In general, hypotheses related to resource distribution and abundance, predation risk, and population density explain both intraspecific and interspecific social variation among caviomorphs. However, some factors appear more important than others do (e.g., food abundance versus population density in determining space use, and predation risk and burrowing costs versus food resources in determining group size), and statistical tools and experimental approaches may enable us to parse out those differences. Nonetheless, the 17 species for which data exist represent a small proportion of the taxon, which numbers over 200 species. These species also occupy a small fraction of the diverse geographic and ecological ranges found across South and Central America. Such diversity can help us understand not only species that display flexibility in social organization but also those species that experience variable conditions and yet may be limited in their ability to respond to those conditions. Although these studies may prove more challenging, they ultimately provide a more comprehensive picture of how and why species respond or do not respond to changes in their environments. The ability to modify behavior in response to changes in environmental conditions may prove essential to these species' persistence in light of anthropogenic changes to their habitats.

Future directions

Technology is constantly increasing our ability to collect, synthesize, and analyze data. Here, we highlight recent technologies and methodological approaches that can advance our understanding of caviomorph social organization at multiple levels of analysis.

Comparative studies

A major focus of sociobiology is to understand the environmental context and phylogenetic constraints that promote convergence and divergence in social evolution between lineages, as well as factors that select for social behavior within lineages. Advancements in genetic sequencing, together with more and better morphological data, allow evolutionary biologists to construct better resolved phylogenies for rodents in general (Blanga-Kanfi et al. 2009) and caviomorphs specifically (Honeycutt et al. 2003; Ojeda et al., this volume; Opazo 2005; Upham & Patterson 2012; Upham et al. 2013). These phylogenies coupled with datasets of social systems (e.g., Appendix 1) will allow researchers to determine the phylogenetic distribution of social systems and unique evolutionary transitions (e.g., Lukas & Clutton-Brock 2013) that give rise to the diversity of social systems across species. Phylogenetic analyses can allow researchers to decipher convergence from divergence in ecology and life history traits and their relationship to social systems not only within caviomorphs but also between caviomorphs and other rodent lineages. High resolution climate data extracted from species' geographic range maps will allow researchers to test hypotheses regarding contributions of environmental change, patchiness, and environmental uncertainty to social systems across species (Jetz & Rubenstein 2011).

Additional field studies on species that lack information of basic biology and social behavior are required to reduce biases in comparative data. For example, tucos are overrepresented in a dataset used to examine social monogamy in mammals (Lukas & Clutton-Brock 2013). Furthermore, small-bodied, diurnal caviomorphs from temperate regions (e.g., degus, maras, and cavies) are generally better studied than smaller, nocturnal tropical species in the family Echimyidae. Surprisingly, little is known of the social systems of the relatively large and arboreal porcupines (Erethizontidae), including the North American porcupine (*Erethizon dorsatum*).

Convergence with other rodent lineages

Despite millions of years of evolutionary divergence among the major rodent lineages (Blanga-Kanfi et al. 2009) resulting in different life history strategies, we see remarkable convergence in social systems between temperate zone caviomorphs and Nearctic ground squirrels (i.e., ground squirrels, marmots, *Marmota* spp., and prairie dogs, *Cynomys* spp. in the family Sciuridae). Social species in both lineages exhibit similar ecological lifestyles including large body size, diurnal activity, and burrowing behavior (Hare & Murie 2007). Branch (1993) specifically noted that the social behavior of plains vizcachas (*Lagostomus maximus*) was comparable to that of black-tailed prairie dogs (*C. ludovicianus*), including similarities in space use, group formation, and interactions within and between groups, and both species occupy similar grassland habitats on separate continents. To better understand similarities and differences between these apparently convergent lineages, similar comparisons could be made between social caviomorphs and ground-dwelling sciurids inhabiting similar habitats.

Another example of convergence occurs between caviomorphs and mole rats, members of the family Bathyergidae. Caviomorphs and bathyergids belong to the same infraorder Histricognathi. Similar to tuco-tucos, most mole rats (or blesmols) are solitary. However, two species, the damaraland belsmo (*Fukomys damarensis*) and the naked mole-rat (*Heterocephalus glaber*) exhibit eusociality, a social system unique among mammals (Lacey & Sherman 2007). Some mole-rat species live in family groups, and the degree of reproductive skew varies across species (Lacey & Sherman 2007). Social, subterranean, or fossorial caviomorphs are plural breeders in contrast to some bathyergids that exhibit division of labor and high reproductive skew within groups. Despite these differences in social system, similarities in environmental pressures including soil distribution and underground food availability appear to have permitted the rise of group living in these taxa (Lacey & Sherman 2007). Indeed, a recent phylogenetic comparative study revealed that sociality within hystricognath rodents has converged multiple times (Sobrero et al. 2014).

In his classic book, Evolutionary Ecology (1999), Pianka noted that similar ecological conditions in different biomes sometimes result in strikingly similar adaptations despite independent evolution. He also cautioned that emphasis on seemingly convergent similarities often undermine the inevitable dissimilarities between supposed ecological equivalents. Life history strategies differ between caviomorphs and ground-dwelling squirrels and are conserved phylogenetically (Ojeda et al., this volume). Caviomorphs typically have long gestation times, short lactation times, and produce precocial offspring, whereas sciuromorphs have short gestation times, long lactation times, and produce altricial young (Ernest 2003). These differences in life history have consequences for offspring care. Few social squirrels exhibit allonursing (Riedman 1982), whereas several plurally breeding caviomorphs do

(Appendix 1). Perhaps allonursing can persist due to short lactation times required for precocial species, as reported for primates that produce precocial young (Isler & van Schaik 2012). Comparative studies of the major rodent lineages provide unique opportunities to understand how similar environmental selection pressures interacting with phylogenetic, developmental, and morphological constraints influence the evolution of sociality.

New techniques for collecting and analyzing social interaction data

Traditionally, most studies of social behavior in caviomorphs, and rodents in general, focused on group size as the experimental unit (e.g., Macdonald et al. 2007), quantifying groups through visual observation or using radiotelemetry or trapping to determine space use and overlap (e.g., Hayes et al. 2009; Cutrera et al. 2010; Tassino et al. 2011). Although these techniques have yielded a wealth of information, their limitations include the necessity for observers to be present in the field, the possibility of misidentifying individuals, and potential bias toward habituated individuals. Furthermore, social interactions vary both within and among groups (Maher 2009), and traditional techniques may ignore or miss this level of social heterogeneity. Recently, several developments in technology and statistical analysis offer opportunities to develop more detailed or comprehensive understanding of social behavior.

Social network analysis provides a valuable tool to quantify social interactions, increasing resolution and sample sizes (Wey et al. 2008; Whitehead 2008). Software to analyze social network data, e.g., SOCPROG in MATLAB (Whitehead 2009) and igraph in R (Csardi & Nepusz 2006), provides similar network statistics (e.g., strength, degree), which make comparisons possible both within and between species (e.g., meta-analyses). Methods to assess orderliness or transitivity of dominance (McDonald & Shizuka 2013) can provide insight into species that form hierarchical societies (e.g., *C. porcellus*, *C. talarum*). Nonetheless, social network analysis still requires data on interactions between individuals, which can be limited by the number of observers and hours spent in the field.

Proximity loggers (e.g., Encounternet) enable researchers to obtain high-resolution accounts of individual interactions spatially and temporally without having to physically observe animals in the field (Prange et al. 2006; Hamede et al. 2009). This technique can be helpful for nocturnal, fossorial or semifossorial, or cryptic species as well as diurnal species in which weather or other logistical concerns impact data collection. However, users must be aware of limitations such as differences in performance across data loggers and independence of the data points (Boyland et al. 2013). Moreover, dominance and social hierarchies cannot be inferred from association data provided by proximity loggers.

Multiple hypothesis testing

The concept of evaluating multiple hypotheses to explain behavior patterns goes back to the early days of behavioral ecology, and some of the best known examples involve rodents, e.g., Belding's ground squirrels, *Spermophilus beldingi* (Sherman 1977), and prairie dogs, *C. leucurus* and *C. ludovicianus* (Hoogland 1981). Since then, researchers have amassed an impressive tool kit of statistical methods to test multiple hypotheses, including model selection using information criteria (Burnham & Anderson 2002) and likelihood ratio tests (Johnson & Omland 2004). Nevertheless, as with any method, researchers must use them judiciously. In particular, the number of hypotheses to test should be reasonable and include some justification prior to analysis (Dochtermann & Jenkins 2011). Hypotheses should fit within the natural history of the species, i.e., they must be biologically relevant (Dochtermann & Jenkins 2011). Furthermore, hypotheses should address the same level of analysis, i.e., proximate or ultimate, and not address complementary aspects of the same phenomenon, which can lead to misleading or erroneous conclusions (Holekamp & Sherman 1989; Dochtermann & Jenkins 2011). Used wisely, multimodel inference provides the opportunity to understand complex interactions in social systems.

Integrating laboratory and field approaches

Not only have we developed technology to collect data and statistical approaches to analyze those data, but we also have made progress toward integrating laboratory and field approaches to answer questions about social systems. Current research on caviomorphs is exploring the underlying hormonal mechanisms related to stress responses, aggression, mating systems, and sociality (Hayes et al. 2011). Typically, these studies occur either in the field or in the lab. For example, guinea pigs have been widely used in laboratory studies of hormones and development (Sachser et al. 2013) but less commonly studied in natural settings. Researchers now combine lab and field approaches to provide a more integrated view of social behavior and the resulting social systems. Thus far, most work has focused on glucocorticoids and subsequent effects on fitness in just one species, the degu (Ebensperger et al. 2011; Quirici et al. 2011b; Ebensperger et al. 2013). The study of glucocorticoids can provide additional insights into phenomena relevant to the maintenance and evolution of sociality, including sex allocation and personality, by exploring activation of the hypothalamic-pituitary-adrenal axis including potential epigenetic effects that can contribute to intraspecific variation (Ryan et al. 2012; Dantzer et al. 2013; Clary et al. 2014).

Furthermore, we have little information about the significance of other catecholaminergic stress pathways in any species.

Results from a study of testosterone levels in degus reveal the importance of combining field and lab studies (Soto-Gamboa et al. 2005). Although testosterone levels varied seasonally in both field and laboratory-housed males, wild males had higher testosterone levels compared to those of lab males, and resident males also had higher cortisol levels. Thus, by focusing only on lab-reared animals, we may lose valuable information about the role of social interactions in the natural setting.

Research on links between stress hormones (glucocorticoids) and fitness has been expanded to include colonial tuco-tucos, a species that varies in social organization (Woodruff et al. 2010; Woodruff et al. 2013). Some yearling females of this species live and breed alone, whereas other yearling females forego dispersal and breed communally. By combining lab and field approaches, biologists could examine natural variation and control conditions by randomly assigning females to live alone or in groups (Woodruff et al. 2013). These results provide a deeper understanding of the role of social environment on levels of glucocorticoids.

Not all species may be amenable to lab studies; however, our broad scale assessment of field studies may reveal candidate species for further investigation in the lab (e.g., Ardiles et al. 2013). Furthermore, field-based experimental manipulations offer great potential for assessing effects of both environmental and social variables on the expression of social behavior under naturalistic conditions (Hare and Murie 2007).

Conclusions

Decades ago, field studies of sciurid rodents contributed to models of the evolution of social behavior in mammals (Michener 1983; Armitage 1999), and studies of bathyergid rodents opened our eyes to eusocial societies in mammals with those evident in the insect order Hymenoptera (Faulkes et al. 1997; Lacey & Sherman 2007). Given the numbers of species and their diversity of ecological lifestyles, caviomorphs have the potential to contribute to the rich history of research on rodent sociality, advancing our understanding of social evolution in general. Many caviomorphs are small-bodied and diurnal, making them ideal model organisms for studying social behavior in natural settings.

Acknowledgements

We thank L. Ebensperger and L. Hayes for the opportunity to contribute to this volume. We also thank J. Hare and an anonymous reviewer for comments on a previous version. JRB was supported by a Shadle Fellowship from the American Society of Mammalogists.

References

Adler, G. H. 2011: Spacing patterns and social mating systems of echimyid rodents. Journal of Mammalogy 92, 31-38.

Adrian, O., Brockmann, I., Hohoff, C. & Sachser, N. 2005: Paternal behaviour in wild guinea pigs: a comparative study in three closely related species with different social and mating systems. Journal of Zoology, London 265, 97-105.

Adrian, O., Kaiser, S., Sachser, N., Jandewerth, P., Löttker, P., Epplen, J. T. & Hennessy, M. B. 2008: Female influences on pair formation, reproduction and male stress responses in a monogamous cavy (*Galea monasteriensis*). Hormones and Behavior 53, 403-412.

Adrian, O. & Sachser, N. 2011: Diversity of social and mating systems in cavies: a review. Journal of Mammalogy 92, 39-53.

Alexander, R. D. 1974: The evolution of social behavior. Annual Review of Ecology and Systematics 5, 325-383.

Alexander, R. M. 2003: A rodent as big as a buffao. Science 301, 1678-1679.

Aliaga-Rossel, E., Kays, R. W. & Fragoso, J. M. V. 2008: Home-range use by the Central American agouti (*Dasyprocta punctata*) on Barro Colorado Island, Panama. Journal of Tropical Ecology 24, 367-374.

Ardiles, A. O., Ewer, J., Acosta, M. L., Kirkwood, A., Martinez, A. D., Ebensperger, L. A., Bozinovic, F., Lee, T. M. & Palacios, A. G. 2013: *Octodon degus* (Molina 1782): A model in comparative biology and biomedicine. Cold Spring Harbor Protocols 2013, pdb.emo071357.

Armitage, K. B. 1999: Evolution of sociality in marmots. Journal of Mammalogy 80, 1-10.

Asher, M., Spinelli De Oliveira, E. & Sachser, N. 2004: Social system and spatial organization of wild guinea pigs (*Cavia aperea*) in a natural population. Journal of Mammalogy 85, 788-796.

Beck-King, H., Von Helversen, O. & Beck-King, R. 1999: Home range, population density, and food resources of *Agouti paca* (Rodentia: Agoutidae) in Costa Rica: a study using alternative methods. Biotropica 31, 675-685.

Becker, M. I., De Ioannes, A. E., León, C. & Ebensperger, L. A. 2007: Females of the communally breeding rodent, *Octodon degus*, transfer antibodies to their offspring during pregnancy and lactation. Journal of Reproductive Immunology 74, 68-77.

Bekoff, M., Daniels, T. J. & Gittleman, J. L. 1984: Life history patterns and the comparative social ecology of carnivores. Annual Review of Ecology and Systematics 15, 191-232.

Blanga-Kanfi, S., Miranda, H., Penn, O., Pupko, T., Debry, R. W. & Huchon, D. 2009: Rodent phylogeny revised: analysis of six nuclear genes from all major rodent clades. BMC Evolutionary Biology 9, 71.

Blumstein, D. T. & Armitage, K. B. 1998: Life history consequences of social complexity: a comparative study of ground-dwelling sciurids. Behavioral Ecology 9, 8-19.

Borowski, A. 2009: *Galea musteloides*. Animal Diversity Web. http://animaldiversity.ummz.umich.edu/accounts/Galea_musteloides/.

Boyland, N. K., James, R., Mlynski, D. T., Madden, J. R. & Croft, D. P. 2013: Spatial proximity loggers for recording animal social networks: consequences of inter-logger variation in performance. Behavioral Ecology and Sociobiology 67, 1877-1890.

Branch, L. C. 1993: Social organization and mating system of the plains viscacha (*Lagostomus maximus*). Journal of Zoology, London 229, 473-491.

Branch, L. C., Villarreal, D. & Fowler, G. S. 1993: Recruitment, dispersal, and group fusion in a declining population of the plains vizcacha (*Lagostomus maximus*; Chincillidae). Journal of Mammalogy 74, 9-20.

Brashares, J. S. & Arcese, P. 2002: Role of forage, habitat and predation in the behavioural plasticity of a small African antelope. Journal of Animal Ecology 71, 626-638.

Brown, J. L. 1964: The evolution of diversity in avian territorial systems. Wilson Bulletin 76, 160-169.

Burger, J. R., Chesh, A. S., Castro, R. A., Tolhuysen, L. O., Torre, I., Ebensperger, L. A. & Hayes, L. D. 2009: The influence of trap type on evaluating population structure of the semifossorial and social rodent *Octodon degus*. Acta Theriologica 54, 311-320.

Burnham, K. P. & Anderson, D. R. 2002: Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York.

Busch, C., Malizia, A. I., Scaglia, O. A. & Reig, O. A. 1989: Spatial distribution and attributes of a population of *Ctenomys talarum* (Rodentia: Octodontidae). Journal of Mammalogy 70, 204-208.

Chartier, K. 2004: *Microcavia australis*. Animal Diversity Web. http://animaldiversity.ummz.umich.edu/accounts/Microcavia_australis/.

Clary, D., Skyner, L. J., Ryan, C. P., Gardiner, L. E., Anderson, W. G. & Hare, J. F. 2014: Shyness-boldness, but not exploration, predicts glucocorticoid stress response in Richardson's ground squirrels (*Urocitellus richardsonii*). Ethology 120, 1101-1109.

Clutton-Brock, T. H. 1974: Primate social organization and ecology. Nature 250, 539-542.

Clutton-Brock, T. H. & Harvey, P. H. 1977: Primate ecology and social organization. Journal of Zoology 183, 1-39.

Contreras, L. C. 1986: Bioenergetics and distribution of fossorial *Spalacopus cyanus* (Rodentia): thermal stress, or cost of burrowing. Physiological Zoology 59, 20-28.

Corriale, M. J., Muschetto, E. & Herrera, E. A. 2013: Influence of group sizes and food resources in home-range sizes of capybaras from Argentina. Journal of Mammalogy 94, 19-28.

Csardi, G. & Nepusz, T. 2006: The igraph software package for complex network research. Interjournal, Complex Systems 1695, 1-9.

Cutrera, A. P., Antinuchi, C. D., Mora, M. S. & Vassallo, A. I. 2006: Home-range and activity patterns of the South American subterranean rodent *Ctenomys talarum*. Journal of Mammalogy 87, 1183-1191.

Cutrera, A. P., Mora, M. S., Antenucci, C. D. & Vassallo, A. I. 2010: Intra- and interspecific variation in home-range size in sympatric tuco-tucos, *Ctenomys australis* and *C. talarum*. Journal of Mammalogy 91, 1425-1434.

D'Elia, G. 1999: *Myocastor coypus*. Animal Diversity Web. http://animaldiversity.ummz.umich.edu/accounts/Myocastor_coypus/.

Dantzer, B., Newman, A. E. M., Boonstra, R., Palme, R., Boutin, S., Humphries, M. M. & Mcadam, A. G. 2013: Density triggers maternal hormones that increase adaptive offspring growth in a wild mammal. Science 340, 1215-1217.

De Almeida, A. J., Freitas, M. M. F. & Talamoni, S. A. 2013: Use of space by the Neotropical caviomorph rodent *Thrichomys apereoides* (Rodentia: Echimyidae). Zoologia 30, 35-42.

Decker, J. 2000: *Dasyprocta punctata*. Animal Diversity Web. http://animaldiversity.ummz.umich.edu/accounts/Dasyprocta_punctata/.

Denena, M. M., Manning, R. W. & Simpson, T. R. 2003: Home range and movement of nutria (*Myocastor coypus*) at Spring Lake in central Texas, with anecdotal comments on the American beaver (*Castor canadensis*) of the same area. Occasional papers Museum of Texas Tech University, 1-11.

Dochtermann, N. & Jenkins, S. H. 2011: Developing multiple hypotheses in behavioral ecology. Behavioral Ecology and Sociobiology 65, 37-45.

Dubost, G. 1988: Ecology and social life of the red acouchy, *Myoprocta exilis*; comparison with the orange-rumped agouti, *Dasyprocta leporina*. Journal of Zoology 214, 107-123.

Dunnum, J. L. & Salazar-Bravo, J. 2004: *Dactylomys boliviensis*. Mammalian species, 1-4.

Ebensperger, L. A. 2001: A review of the evolutionary causes of rodent group-living. Acta Theriologica 46, 115-144.

Ebensperger, L. A. & Blumstein, D. T. 2006: Sociality in New World hystricognath rodents is linked to predators and burrow digging. Behavioral Ecology 17, 410-418.

Ebensperger, L. A. & Bozinovic, F. 2000: Communal burrowing in the hystricognath rodent, *Octodon degus*: a benefit of sociality? Behavioral Ecology and Sociobiology 47, 365-369.

Ebensperger, L. A., Chesh, A. S., Castro, R. A., Tolhuysen, L. O., Quirici, V., Burger, J. R. & Hayes, L. D. 2009: Instability rules social groups in the communal breeder rodent *Octodon degus*. Ethology 115, 540-554.

Ebensperger, L. A. & Cofré, H. 2001: On the evolution of group-living in the New World cursorial hystricognath rodents. Behavioral Ecology 12, 227-236.

Ebensperger, L. A., Hurtado, M. J. & Leon, C. 2007: An experimental examination of the consequences of communal versus solitary breeding on maternal condition and the early postnatal growth and survival of degu, *Octodon degus*, pups. Animal Behaviour 73, 185-194.

Ebensperger, L. A., Hurtado, M. J., Soto-Gamboa, M., Lacey, E. A. & Chang, A. T. 2004: Communal nesting and kinship in degus (*Octodon degus*). Naturwissenschaften 91, 391-395.

Ebensperger, L. A., Ramirez-Estrada, J., Leon, C., Castro, R. A., Tolhuysen, L. O., Sobrero, R., Quirici, V., Burger, J. R., Soto-Gamboa, M. & Hayes, L. D. 2011: Sociality, glucocorticoids and direct fitness in the communally rearing rodent, *Octodon degus*. Hormones and Behavior 60, 346-352.

Ebensperger, L. A., Sobrero, R., Quirici, V., Castro, R. A., Tolhuysen, L. O., Vargas, F., Burger, J. R., Quispe, R., Villavicencio, C. P., Vasquez, R. A. & Hayes, L. D. 2012: Ecological drivers of group living in two populations of the communally rearing rodent, *Octodon degus*. Behavioral Ecology and Sociobiology 66, 261-274.

Ebensperger, L. A., Tapia, D., Ramirez-Estrada, J., Leon, C., Soto-Gamboa, M. & Hayes, L. D. 2013: Fecal cortisol levels predict breeding but not survival of females in the short-lived rodent, *Octodon degus*. General and Comparative Endocrinology 186, 164-171.

Ebensperger, L. A., Taraborelli, P., Giannoni, S. M., Hurtado, M. J., León, C. & Bozinovic, F. 2006: Nest and space use in a highland population of the southern mountain cavy (*Microcavia australis*). Journal of Mammalogy 87, 834-840.

Ebensperger, L. A., Veloso, C. & Wallem, P. K. 2002: Do female degus communally nest and nurse their pups? Journal of Ethology 20, 143-146.

Ebensperger, L. A. & Wallem, P. K. 2002: Grouping increases the ability of the social rodent, *Octodon degus*, to detect predators when using exposed microhabitats. Oikos 98, 491-497.

Eisenberg, J. F. 1989: Mammals of the Neotropics. v. 1. The northern neotropics: Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana. University of Chicago Press, Chicago.

Emlen, S. T. 1982: The evolution of helping. I. An ecological constraints model. American Naturalist 119, 29-39.

Emlen, S. T. & Oring, L. W. 1977: Ecology, sexual selection, and the evolution of mating systems. Science 197, 215-223.

Emsens, W.-J., Suselbeek, L., Hirsch, B. T., Kays, R. W., Winkelhagen, A. J. S. & Jansen, P. A. 2013: Effects of food availability on space and refuge use by a Neotropical scatterhoarding rodent. Biotropica 45, 88-93.

Endries, M. J. & Adler, G. H. 2005: Spacing patterns of a tropical forest rodent, the spiny rat (*Proechimys semispinosus*), in Panama. Journal of Zoology (London) 265, 147-155.

Ernest, S. M. 2003: Life history characteristics of placental nonvolant mammals. Ecology 84, 3402-3402.

Faulkes, C. G. & Bennett, N. C. 2007: African mole-rats: social and ecological diversity. In: Rodent societies: an ecological and evolutionary perspective. (Wolff, J. O. & Sherman, P. W., eds). University of Chicago Press, Chicago. pp. 427-437.

Faulkes, C. G., Bennett, N. C., Bruford, M. W., O'brien, H. P., Aguilar, G. H. & Jarvis, J. U. M. 1997: Ecological constraints drive social evolution in the African mole-rats. Proceedings of the Royal Society of London B 264, 1619-1627.

Feldhamer, G. A., Drickamer, L. C., Vessey, S. H. & Merritt, J. F. 2004: Mammalogy: adaptation, diversity, and ecology, 2nd edn. McGraw-Hill, New York.

Fisher, D. O. & Owens, I. P. F. 2000: Female home range size and the evolution of social organization in macropod marsupials. Journal of Animal Ecology 69, 1083-1098.

Getz, L. L., Mcguire, B. & Carter, C. S. 2005: Social organization and mating system of free-living prairie voles *Microtus ochrogaster*: a review. Acta Zoologica Sinica 51, 178-186.

Gittleman, J. L. 1989: Carnivore behavior, ecology, and evolution. Comstock Publishing Associates, Ithaca.

Graur, D., Hide, W. A. & Li, W. H. 1991: Is the guinea pig a rodent? Nature 351, 649-652.

Guichon, M. B., Righi, C. F., Cassini, G. H. & Cassini, M. H. 2003: Social behavior and group formation in the coypu (*Myocastor coypus*) in the Argentinean pampas. Journal of Mammalogy 84, 254-262.

Hamede, R. K., Bashford, J., Mccallum, H. & Jones, M. 2009: Contact networks in a wild Tasmanian devil (*Sarcophilus harrisii*) population: using social network analysis to reveal seasonal variability in social behaviour and its implications for transmission of devil facial tumour disease. Ecology Letters 12, 1147-1157.

Hare, J. F. & Murie, J. O. 2007: Ecology, kinship, and ground squirrel sociality: insights from comparative analysis. In: Rodent societies: an ecological and evolutionary perspective. (Wolff, J. O. & Sherman, P. W., eds). University of Chicago Press, Chicago, Illinois. pp. 345-355.

Hayes, L. D., Burger, J. R., Soto-Gamboa, M., Sobrero, R. & Ebensperger, L. A. 2011: Towards an integrative model of sociality in caviomorph rodents. Journal of Mammalogy 92, 65-77.

Hayes, L. D., Chesh, A. S., Castro, R. A., Tolhuysen, L. O., Burger, J. R., Bhattacharjee, J. & Ebensperger, L. A. 2009: Fitness consequences of group living in the degu *Octodon degus*, a plural breeder rodent with communal care. Animal Behaviour 78, 131-139.

Hayes, L. D., Chesh, A. S. & Ebensperger, L. A. 2007: Ecological predictors of range areas and use of burrow systems in the diurnal rodent, *Octodon degus*. Ethology 113, 155-165.

Hayes, L. D. & Ebensperger, L. A. 2011: Caviomorph rodent social systems: an introduction. Journal of Mammalogy 92, 1-2.

Herrera, E. A. 2013: Capybara social behavior and use of space: patterns and processes. In: Capybara: Biology, use and conservation of an exceptional Neotropical species. (Moreira, J. R., Ferraz, K. M. P. M. B., Herrera, E. A. & Macdonald, D. W., eds). Springer, New York. pp. 195-207.

Herrera, E. A. & Macdonald, D. W. 1987: Group stability and the structure of a capybara population. Symposia of the Zoological Society of London 58, 115-130.

-. 1989: Resource utilization and territoriality in group-living capybaras (*Hydrochoerus hydrochaeris*). Journal of Animal Ecology 58, 667-679.

Herrera, E. A., Salas, V., Congdon, E. R., Corriale, M. J. & Tang-Martinez, Z. 2011: Capybara social structure: variations on a fixed theme. Journal of Mammalogy 92, 12-20.

Hohoff, C., Solmsdorff, K., Löttker, P., Kemme, K., Epplen, J. T., Cooper, T. G. & Sachser, N. 2002: Monogamy in a new species of wild guinea pigs (*Galea* sp.). Naturwissenschaften 89, 462-465.

Holekamp, K. E. & Sherman, P. W. 1989: Why male ground squirrels disperse: A multilevel analysis explains why only males leave home. American Scientist 77, 232-239.

Honeycutt, R. L., Rowe, D. L. & Gallardo, M. H. 2003: Molecular systematics of the South American caviomorph rodents: relationships among species and genera in the family Octodontidae. Molecular Phylogenetics and Evolution 26, 476-489.

Hoogland, J. L. 1981: The evolution of coloniality in white-tailed prairie dogs and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *Cynomys ludovicianus*). Ecology 62, 252-272.

Isler, K. & Van Schaik, C. P. 2012: Allomaternal care, life history and brain size evolution in mammals. Journal of Human Evolution 63, 52-63.

Jaimes, M. 2007: *Myoprocta acouchy*. Animal Diversity Web. http://animaldiversity.ummz.umich.edu/accounts/Myoprocta_acouchy/.

Jarman, P. J. 1974: The social organisation of antelope in relation to their ecology. Behaviour 48, 215-266.

Jetz, W. & Rubenstein, D. R. 2011: Environmental uncertainty and the global biogeography of cooperative breeding in birds. Current Biology 21, 72-78.

Johnson, D. D. P., Kays, R., Blackwell, P. G. & Macdonald, D. W. 2002: Does the resource dispersion hypothesis explain group living? Trends in Ecology and Evolution 17, 563-570.

Johnson, J. B. & Omland, K. S. 2004: Model selection in ecology and evolution. Trends in Ecology & Evolution 19, 101-108.

Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'dell, J., Orme, C. D. L., Safi, K., Sechrest, W., Boakes, E. H., Carbone, C., Connolly, C., Cutts, M. J., Foster, J. K., Grenyer, R., Habib, M., Plaster, C. A., Price, S. A., Rigby, E. A., Rist, J., Teacher, A., Bininda-Emonds, O. R. P., Gittleman, J. L., Mace, G. M., Purvis, A. & Michener, W. K. 2009: PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90, 2648-2648.

Jorge, M. S. P. & Peres, C. A. 2005: Population density and home range size of red-rumped agoutis (*Dasyprocta leporina*) within and outside a natural Brazil nut stand in southeastern Amazonia. Biotropica 37, 317-321.

Juni, E. 2011: *Myoprocta pratti*. Animal Diversity Web. http://animaldiversity.ummz.umich.edu/accounts/Myoprocta_pratti/.

Kappeler, P. M. & Van Schaik, C. P. 2002: Evolution of primate social systems. International Journal of Primatology 23, 707-740.

Kleiman, D. G. 1971: The courtship and copulatory behaviour of the green acouchi, *Myoprocta pratti*. Zeitschrift fur Tierpsychologie 29, 259-278.

Kleiman, D. G. 1972: Maternal behaviour of the green acouchi (*Myoprocta pratti* Pocock), a South American caviomorph rodent. Behaviour 43, 48-84.

Komers, P. E. & Brotherton, P. N. M. 1997: Female space use is the best predictor of monogamy in mammals. Proceedings of the Royal Society of London. Series B: Biological Sciences 264, 1261-1270.

Koprowski, J. L. 1998: Conflict between the sexes: a review of social and mating systems of the tree squirrels. In: Ecology and evolutionary biology of tree squirrels. (Steele, M. A., Merritt, J. F. & Zegers, D. A., eds). Virginia Museum of Natural History. pp. 33-41.

Krause, J. & Godin, J.-G. J. 1995: Predator preferences for attacking particular prey group sizes: consequences for predator hunting success and prey predation risk. Animal Behaviour 50, 465-473.

Kraus, C., Kunkele, J. & Trillmich, F. 2003: Spacing behaviour and its implications for the mating system of a precocial small mammal: an almost asocial cavy *Cavia magna*? Animal Behaviour 66, 225-238.

Lacey, E. A. 2004: Sociality reduces individual direct fitness in a communally breeding rodent, the colonial tuco-tuco (*Ctenomys sociabilis*). Behavioral Ecology and Sociobiology 56, 449-457.

Lacey, E. A., Braude, S. H. & Wieczorek, J. R. 1997: Burrow sharing by colonial tuco-tucos (*Ctenomys sociabilis*). Journal of Mammalogy 78, 556-562.

Lacey, E. A. & Ebensperger, L. A. 2007: Social structure in octodontid and ctenomyid rodents. In: Rodent societies: an ecological and evolutionary perspective. (Wolff, J. O. & Sherman, P. W., eds). University of Chicago Press, Chicago, Illinois. pp. 403-415.

Lacey, E. A. & Sherman, P. W. 2007: The ecology of sociality in rodents. In: Rodent societies: an ecological and evolutionary perspective. (Wolff, J. O. & Sherman, P. W., eds). University of Chicago Press, Chicago, Illinois. pp. 243-254.

Lacey, E. A. & Wieczorek, J. R. 2003: Ecology of sociality in rodents: a ctenomyid perspective. Journal of Mammalogy 84, 1198-1211.

Lacher, J., T.E. 1981: The comparative social behavior of *Kerodon rupestris* and *Galea spixii* and the evolution of behavior in the Caviidae. Bulletin of Carnegie Museum of Natural History 17, 1-71.

Lagos, V. O., Contreras, L. C., Meserve, P. L., Gutierrez, J. R. & Jaksic, F. M. 1995: Effects of predation risk on space use by small mammals: a field experiment with a Neotropical rodent. Oikos 74, 259-264.

Langbein, J. & Thirgood, S. J. 1989: Variation in mating systems of fallow deer (*Dama dama*) in relation to ecology. Ethology 83, 195-214.

Laval, R. K. 1976: Voice and habitat of *Dactylomys dactylinus* (Rodentia: Echimyidae) in Ecuador. Journal of Mammalogy 57, 402-404.

Lott, D. F. 1991: Intraspecific variation in the social systems of wild vertebrates. Cambridge University Press, Cambridge, United Kingdom.

Lucia, K. E., Keane, B., Hayes, L. D., Lin, Y. K., Schaefer, R. L. & Solomon, N. G. 2008: Philopatry in prairie voles: an evaluation of the habitat saturation hypothesis. Behavioral Ecology 19, 774-783.

Lukas, D. & Clutton-Brock, T. H. 2013: The evolution of social monogamy in mammals. Science 341, 526-530.

Macdonald, D. W. 1981: Dwindling resources and the social behaviour of capybaras (*Hydrochoerus hydrochaeris*) (Mammalia). Journal of Zoology, London 194, 371-391.

-. 1983: The ecology of carnivore social behaviour. Nature 301, 379-384.

Macdonald, D. W., Herrera, E. A., Taber, A. B. & Moreira, J. R. 2007: Social organization and resource use in capybaras and maras. In: Rodent societies: an ecological and evolutionary perspective. (Wolff, J. O. & Sherman, P. W., eds). University of Chicago Press, Chicago, Illinois. pp. 393-402.

Macdonald, G. 2013: *Cuniculus paca*. Animal Diversity Web. http://animaldiversity.ummz.umich.edu/accounts/Cuniculus_paca/.

Maher, C. R. 2009: Effects of relatedness on social interaction rates in a solitary marmot. Animal Behaviour 78, 925-933.

Maher, C. R. & Burger, J. R. 2011: Intraspecific variation in space use, group size, and mating systems of caviomorph rodents. Journal of Mammalogy 92, 54-64.

Maher, C. R. & Lott, D. F. 2000: A review of ecological determinants of territoriality within vertebrate species. American Midland Naturalist 143, 1-29.

Malizia, A. I. 1998: Population dynamics of the fossorial rodent *Ctenomys talarum* (Rodentia: Octodontidae). Journal of Zoology, London 244, 545-551.

Mann, J., Connor, R. C., Tyack, P. L. & Whitehead, H. 2002: Cetacean societies: field studies of dolphins and whales. University of Chicago Press, Chicago. pp. 448 pp.

Mascow, M. 2011: *Dolichotis patagonum*. Animal Diversity Web. http://animaldiversity.ummz.umich.edu/accounts/Dolichotis_patagonum/.

Mcdonald, D. B. & Shizuka, D. 2013: Comparative transitive and temporal orderliness in dominance networks. Behavioral Ecology 24, 511-520.

McGinnis, L. 2011: *Dasyprocta mexicana*. Animal Diversity Web. http://animaldiversity.ummz.umich.edu/accounts/Dasyprocta_mexicana/.

Michener, G. R. 1983: Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. In: Advances in the study of mammalian behavior. (Eisenberg, J. F. & Kleiman, D. G., eds). American Society of Mammalogists, Stillwater, Oklahoma. pp. 528-572.

Opazo, J. C. 2005: A molecular timescale for caviomorph rodents (Mammalia, Hystricognathi). Molecular Phylogenetics and Evolution 37, 932-937.

Pearson, O. P., Binsztein, N., Boiry, L., Busch, C., Di Pace, M., Gallopin, G., Penchaszadeh, P. & Piantanida, M. J. 1968: Estructura social, distribución espacial y composición por edades de una población de tuco-tucos (*Ctenomys talarum*). Investigaciones Zoologicas Chilenas 13, 47-79.

Pianka, E. R. 1999: Evolutionary ecology. Benjamin Cummings, San Francisco.

Prange, S., Jordan, T., Hunter, C. & Gehrt, S. D. 2006: New radiocollars for the detection of proximity among individuals. Wildlife Society Bulletin 34, 1333-1344.

Quirici, V., Castro, R. A., Ortiz-Tolhuysen, L., Chesh, A. S., Burger, J. R., Miranda, E., Cortes, A., Hayes, L. D. & Ebensperger, L. A. 2010: Seasonal variation in the range areas of the diurnal rodent *Octodon degus*. Journal of Mammalogy 91, 458-466.

Quirici, V., Faugeron, S., Hayes, L. D. & Ebensperger, L. A. 2011a: Absence of kin structure in a population of the group-living rodent *Octodon degus*. Behavioral Ecology 22, 248-254.

-. 2011b: The influence of group size on natal dispersal in the communally rearing and semifossorial rodent, *Octodon degus*. Behavioral Ecology and Sociobiology 65, 787-798.

Randall, J. A. 2007: Environmental constraints and the evolution of sociality in semifossorial desert rodents. In: Rodent societies: an ecological and evolutionary perspective. (Wolff, J. O. & Sherman, P. W., eds). University of Chicago Press, Chicago. pp. 368-379.

Riedman, M. L. 1982: The evolution of alloparental care and adoption in mammals and birds. Quarterly Review of Biology 57, 405-434.

Rivera, D. S., Abades, S. & Ebensperger, L. A. 2014: Sociality of *Octodontomys gliroides* and other octodontid rodents reflect the influence of phylogeny Journal of Mammalogy 95, 968-980.

Rood, J. P. 1972: Ecological and behavioural comparisons of three genera of Argentine cavies. Animal Behaviour Monographs 5, 1-83.

Rubenstein, D. R. 2011: Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. Proceedings of the National Academy of Sciences of the United States of America 108, 10816-10822.

Ryan, C. P., Anderson, W. G., Gardiner, L. E. & Hare, J. F. 2012: Stress-induced sex ratios in ground squirrels: support for a mechanistic hypothesis. Behavioral Ecology 23, 160-167.

Saavedra-Rodríguez, C. A., Kattan, G. H., Osbahr, K. & Hoyos, J. G. 2012: Multiscale patterns of habitat and space use by the Pacarana *Dinomys branickii*: Factors limiting its distribution and abundance. Endangered Species Research 16, 273-281.

Sachser, N. 1986: Different forms of social organization at high and low population densities in guinea pigs. Behaviour 97, 253-272.

Sachser, N., Kaiser, S. & Hennessy, M. B. 2013: Behavioural profiles are shaped by social experience: when, how and why. Philosophical Transactions of the Royal Society B: Biological Sciences 368, 20120344.

Santos, J. W. A. & Lacey, E. A. 2011: Burrow sharing in the desert-adapted torch-tail spiny rat, *Trinomys yonenagae*. Journal of Mammalogy 92, 3-11.

Schaller, G. B. & Gransden Crawshaw Jr., P. 1981: Social organization in a capybara population. Saugetierkundliche Mitteilungen 29, 3-16.

Sherman, P. W. 1977: Nepotism and the evolution of alarm calls. Science 197, 1246-1253.

Sibly, R. M. & Brown, J. H. 2007: Effects of body size and lifestyle on evolution of mammal life histories. Proceedings of the National Academies of Science 104, 17707-17712.

Silva, R. B., Vieira, E. M. & Izar, P. 2008: Social monogamy and biparental care of the neotropical southern bamboo rat (*Kannabateomys amblyonyx*). Journal of Mammalogy 89, 1464-1472.

Silvius, K. M. & Fragoso, J. M. V. 2003: Red-rumped agouti (*Dasyprocta leporina*) home range use in an Amazonian forest: implications for the aggregated distribution of forest trees. Biotropica 35, 74-83.

Slobodchikoff, C. N. 1984: Resources and the evolution of social behavior. In: A new ecology: novel approaches to interactive systems. (Price, P. W., Slobodchikoff, C. N. & Gaud, W. S., eds). John Wiley and Sons, New York, New York. pp. 227-251.

Sobrero, R., Inostroza-Michael, O., Hernández, C. E. & Ebensperger, L. A. 2014: Phylogeny modulates the effects of ecological conditions on group-living across hystricognath rodents. Animal Behaviour 94, 27-34.

Soto-Gamboa, M., Villalon, M. & Bozinovic, F. 2005: Social cues and hormone levels in male *Octodon degus* (Rodentia): a field test of the Challenge Hypothesis. Hormones and Behavior 47, 311-318.

Stallings, J. R., Kierulff, M. C. M. & Silva, L. F. B. M. 1994: Use of space, and activity patterns of Brazilian bamboo rats (*Kannabateomys amblyonyx*) in exotic habitat. Journal of Tropical Ecology 10, 431-438.

Taber, A. B. & Macdonald, D. W. 1992: Spatial organization and monogamy in the mara *Dolichotis patagonum*. Journal of Zoology (London) 227, 417-438.

Taraborelli, P. & Moreno, P. 2009: Comparing composition of social groups, mating system and social behaviour in two populations of *Microcavia australis*. Mammalian Biology 74, 15-24.

Tasse, J. 1986: Maternal and paternal care in the rock cavy, *Kerodon rupestris*, a South American hystricomorph rodent. Zoo Biology 5, 27-43.

Tassino, B., Estevan, I., Garbero, R. P., Altesor, P. & Lacey, E. A. 2011: Space use by Rio Negro tuco-tucos (*Ctenomys rionegrensis*): excursions and spatial overlap. Mammalian Biology 76, 143-147.

Tognelli, M. F., Campos, C. M. & Ojeda, R. A. 2001: *Microcavia australis*. Mammalian species, 1-4.

Travis, S. E., Slobodchikoff, C. N. & Keim, P. 1995: Ecological and demographic effects on intraspecific variation in the social system of prairie dogs. Ecology 76, 1794-1803.

Túnez, J. I., Guichón, M. L., Centrón, D., Henderson, A. P., Callahan, C. & Cassini, M. H. 2009: Relatedness and social organization of coypus in the Argentinean pampas. Molecular Ecology 18, 147-155.

Upham, N. S., Ojala-Barbour, R., M, J. B., Velazco, P. M. & Patterson, B. D. 2013: Transitions between Andean and Amazonian centers of endemism in the radiation of some arboreal rodents. BMC Evolutionary Biology 13, 191.

Upham, N. S. & Patterson, B. D. 2012: Diversification and biogeography of the Neotropical caviomorph lineage Octodontoidea (Rodentia: Hystricognatha). Molecular Phylogenetics and Evolution 63, 417-429.

Viitala, J., Pusenius, J., Ylonen, H., Mappes, T. & Hakkarainen, H. 1996: Social organization and life history strategy in microtines. Proceedings of the I European Congress of Mammalogy, 151-161.

Wey, T., Blumstein, D. T., Shen, W. & Jordan, F. 2008: Social network analysis of animal behaviour: a promising tool for the study of sociality. Animal Behaviour 75, 333-344.

Wey, T. W., Burger, J. R., Ebensperger, L. A. & Hayes, L. D. 2013: Reproductive correlates of social network variation in plurally breeding degus (*Octodon degus*). Animal Behaviour 85, 1407-1414.

Whitehead, H. 2008: Analyzing animal societies: quantitative methods for vertebrate social analysis. University of Chicago Press, Chicago, Illinois.

Whitehead, H. 2009: SOCPROG programs: analysing animal social structures. Behavioral Ecology and Sociobiology 63, 765-778.

Woodroffe, R. & Vincent, A. 1994: Mother's little helpers: patterns of male care in mammals. Trends in Ecology and Evolution 9, 294-297.

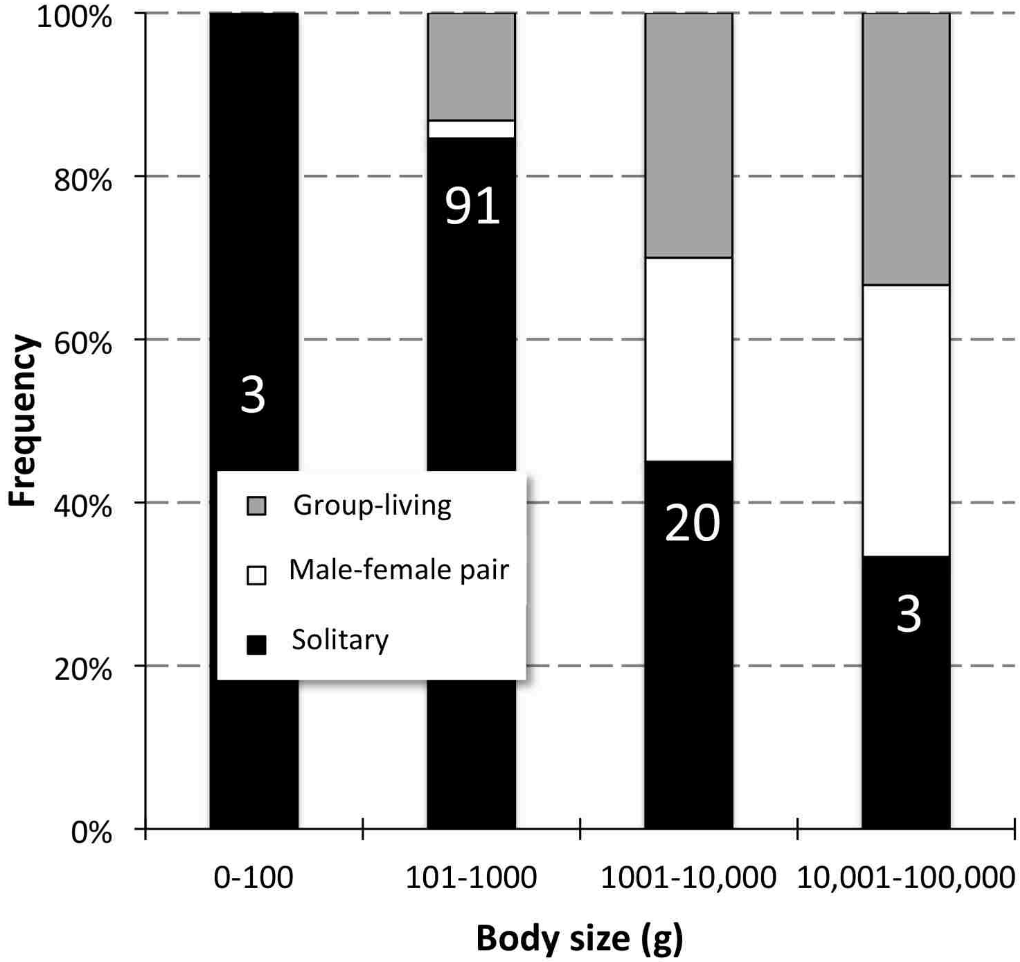
Woodruff, J. A., Lacey, E. A. & Bentley, G. 2010: Contrasting fecal corticosterone metabolite levels in captive and free-living colonial tuco-tucos (*Ctenomys sociabilis*). Journal of Experimental Zoology 313A, 498-507.

Woodruff, J. A., Lacey, E. A., Bentley, G. E. & Kriegsfeld, L. J. 2013: Effects of social environment on baseline glucocorticoid levels in a communally breeding rodent, the colonial tuco-tuco (*Ctenomys sociabilis*). Hormones and Behavior 64, 566-572.

Zenuto, R. R., Lacey, E. A. & Busch, C. 1999a: DNA fingerprinting reveals polygyny in the subterranean rodent *Ctenomys talarum*. Molecular Ecology 8, 1529-1532.

Zenuto, R. R., Malizia, A. I. & Busch, C. 1999b: Sexual size dimorphism, testes size and mating system in two populations of *Ctenomys talarum* (Rodentia: Octodontidae). Journal of Natural History 33, 305-314.

Figure 1: The distribution of social systems for 118 species of caviomorphs over the range of log10 body sizes (J. R. Burger, A. L. Prieto, & L. D. Hayes, unpublished data). The number of species per body size bin is shown in white.



Family	**Species**	**Mating system**	**Breeding system**	**Offspring care**	**Paternal care**	**Sexual size dimorphism**	**Relative home range size (M to F)**	**Home range overlap**	**Group size and composition**	**Activity period**	**Habitat mode**	**Diet**	**Reference**
Caviidae	*Kerodon rupestris*	Resource defense polygyny	Singular breeding?	Biparental	Yes	M=F	NA	Extensive with hierarchical social structures	1M, multiF	D	Burrowing/ rock dens	Herbivorous	1, 2, 3, 4
Caviidae	*Galea monasteriensis*	Social monogamy	Singular breeding	Biparental	Yes	F>M	NA	NA	M, F pairs	D	Burrowing	Herbivorous	3, 5, 6
Caviidae	*Cavia aperea*	Female defense polygyny	Plural breeding	Alloparental	Yes	M>F	M>F	M overlap of multiple F > overlap of F; no M-M overlap	1M, 1-3 F	D/C	Tunneling	Herbivorous	3, 4, 6, 7
Caviidae	*Galea musteloides*	Promiscuity	Plural breeding	Alloparental	No	F>M	M>F	Usually no F-F overlap; M overlap with several F, M	Mixed sex groups with dominant M	D/C	Terrestrial	Herbivorous	3, 4, 6, 8
Caviidae	*Hydrochoerus hydrochaeris*	Polygyny-Promiscuity	Plural breeding	Alloparental	No	F=M	M=F	Within group overlap for both sexes	10-30 individuals of both sexes	D	Semi-aquatic	Herbivorous	9, 10, E. Herrera, pers. comm.
Caviidae	*Microcavia australis*	Promiscuity; polygyny	Plural breeding	Alloparental	No	M=F	M>F	F overlap extensively; M wander among F groups	1–4 breeding F; 1 or 2 breeding M	D	Burrowing	Herbivorous	4, 5, 11, 12, 13
Caviidae	*Dolichotis patagonum*	Social monogamy	Plural breeding	Mother only	No	M>F	M=F	Pairs overlap when foraging; little overlap between pairs; multiple pairs share dens	Members with various sex ratios	D	Burrowing	Herbivorous	4, 9, 10, 14, 15
Chinchillidae	*Lagostomus maximus*	Female defense polygyny	Plural breeding	Alloparental	No	M>F	M=F	Within group overlap of both sexes	Several F with ≥ 1 M	N	Burrowing	Herbivorous	4, 16, 17
Ctenomyidae	*Ctenomys sociabilis*	Polygyny	Plural breeding	Alloparental	No	M=F?	M=F	Extensive within colonies	Several F and adult M	D	Burrowing	Herbivorous	18, 19, 20
Cuniculidae	*Cuniculus paca*	Social monogamy	Singular breeding	Mother only	No	M>F	M=F	Monogamous pairs overlap	Adult M & F with offspring	N	Burrowing	Frugivorous	4, 21, 22
Dasyproctidae	*Dasyprocta punctata*	Social monogamy	Singular breeding	Mother only	No	M=F?	M>F	M-F overlap, F-F overlap, M aggressive	Adult M& F with offspring	D	Terrestrial	Frugivorous	4, 22, 23, 24
Dasyproctidae	*Dasyprocta leporina*	Social monogamy	Singular breeding	Mother only	No	F>M	M=F	Shared by all family members	Monogamous pairs and family groups	D	Terrestrial	Frugivorous	4, 22, 25
Dasyproctidae	*Dasyprocta mexicana*	Social monogamy	Singular breeding	Mother only	No	M=F	M=F	Pairs maintain home range	Monogamous pairs	D	Terrestrial	Frugivorous	4, 22, 26
Dasyproctidae	*Myoprocta acouchy*	Social monogamy	Singular breeding	Mother only	No	M=F	M=F	High within group overlap including both sexes; core areas of activity separate; no intergroup interaction	Family groups	D	Terrestrial	Frugivorous	4, 25, 27
Dasyproctidae	*Myoprocta pratti*	Monogamy	Plural breeding	Alloparental	No	M=F	NA	NA	NA	D/C	Burrowing	Herbivorous	25, 28, 29, 30
Dinomyidae	*Dinomys branickii*	Social monogamy	Singular breeding	Mother only	No	M=F	M=F	Within group overlap	4-5 individuals	N	Terrestrial	Frugivorous	4, 22, 31
Echimyidae	*Kannabateomys amblyonyx*	Social monogamy	Singular breeding	Biparental	Yes	M=F	M=F	Pairs overlap exclusively	M-F pairs with offspring	N?	Arboreal	Herbivorous	32, 33
Echimyidae	*Trinomys yonenagae*	Promiscuity	Plural breeding	Alloparental	Yes	M=F	M=F	Extensive	Same-sex pairs, M-F pairs, and multiple adults of both sexes	N	Burrowing	Herbivorous	34
Echimyidae	*Proechimys semispinosus*	Facultative monogamy, Promiscuity, Polygyny	Singular breeding?	Mother only?	No?	M=F?	M>F	Extensive overlap	NA				35
Myocastoridae	*Myocastor coypus*	Polygyny	Plural breeding	Alloparental	No	M>F	M=F	Extensive within group; territorial between groups	Multiple M, F with dominant M	N	Semiaquatic	Herbivorous	4, 22, 35, 36, 37, 38
Octodontidae	*Octodon degus*	Promiscuity?	Plural breeding	Alloparental	No	M=F	M=F	M-M and M-F overlap; F-F and F-M	Core multiple F, high M turnover	D	Burrowing	Herbivorous	22, 39, 40, 41, 42

Appendix 1: Interspecific variation in social systems of caviomorphs. Abbreviations used: M = male; F = female; N = nocturnal; D = diurnal; C = crepuscular

1(Lacher 1981); 2(Tasse 1986); 3(Adrian & Sachser 2011); 4(Jones et al. 2009); 5(Adrian et al. 2008); 6(Adrian et al. 2005); 7(Asher et al. 2004); 8(Borowski 2009); 9(Herrera et al. 2011); 10(MacDonald et al. 2007); 11(Tognelli et al. 2001); 12(Chartier 2004); 13(Ebensperger et al. 2006); 14(Taber & McDonald 1992); 15(Mascow 2011); 16(Branch 1993); 17(Branch et al. 1993); 18(Lacey & Wieczorek 2003); 19(Lacey & Ebensperger 2007); 20(Lacey et al. 1997); 21(Macdonald 2013); 22(Lukas & Clutton-Brock 2013); 23(Decker 2000); 24(Aliaga-Rossel et al. 2008); 25(Dubost 1988); 26(McGinnis 2011); 27(Jaimes 2007); 28(Kleiman 1971); 29(Kleiman 1972); 30(Juni 2011); 31(Saavedra-Rodríguez et al. 2012); 32(Stallings et al. 1994); 33(Silva et al. 2008); 34(Santos & Lacey 2011); 35(Adler 2011); 36(Guichon et al. 2006); 37(D'Elia 1999); 38(Denena et al. 2003); 39(Ebensperger et al. 2002); 40(Quirici et al. 2010); 41(Wey et al. 2013); 42(Burger et al. 2009); 43(Contreras 1986); 44(Rivera et al. 2014); 45(Sobrero et al. 2014)

Family	Species	Aspect of social organization	Ecological correlate	Habitat	Reference
Caviidae	*Cavia porcellus*	Temporal shift from dominance hierarchy to territoriality	Population density	Captivity	1
Caviidae	*C. aperea*	Temporal shift in home range usage	Predation risk	University of São Paulo campus	2
		Mating system: monogamy, polygyny	Population density, food distribution		2
Caviidae	*C. magna*	Temporal change in overlap, size, shift in core home range area	Water level (direct), population density (indirect)	Wetland surrounded by grassland	3
Caviidae	*Galea musteloides*	Group size	Food abundance	Stone wall, Ñacuñán Biosphere Reserve	4, 5
Caviidae	*Microcavia australis*	Group size	Climate severity, food abundance, quality	Desert	6
Caviidae	*Dolichotis patagonum*	Group size	Food abundance, distribution	Semiarid thorn scrub	7
Caviidae	*Hydrochoerus hydrochaeris*	Temporal changes in home range size; spatial changes in home range overlap	Food abundance	Seasonally flooded grassland	8

Family	Species	Aspect of social organization	Ecological correlate	Habitat	Reference
		Group size	Water availability, population density	Tropical floodplain savanna; seasonally flooded grassland	9–13
Echimyidae	*Proechimys semispinosus*	Temporal change in overlap, size of home ranges	Population density	Tropical moist forest	14
		Mating system: monogamy, promiscuity	Population density		14
Echimyidae	*Thrichomys apereoides*	Temporal shift in daily home range size	Food availability	Semideciduous forest and humid tropical savanna	15
Echimyidae	*Kannabateomys amblyonyx*	Mating system: social monogamy, polygyny	Food distribution		16, 17
Cuniculidae	*Cuniculus paca*	Temporal shift in core home range size	Food availability	Tropical lowland wet forest	18
		Group size	Food abundance	Lowland wet tropical	18
Dasyproctidae	*Dasyprocta leporina*	Temporal shift in core home range size	Food availability	Stands of Brazil nuts; transitional forest between	19, 20

Family	Species	Aspect of social organization	Ecological correlate	Habitat	Reference
				rainforest and savannah	
Dasyproctidae	*D. punctata*	Spatial variation in home range size	Food availability	Tropical moist and semideciduous forest	21, 22
Ctenomyidae	*Ctenomys talarum*	Spatial variation in distribution of home ranges	Population density, environmental heterogeneity	Grassland coastal dunes	23–25
		Spatial variation in home range size	Soil characteristics	Coastal sand dunes and grasslands	26
		Mating system (degree of polygyny)	Food resources, soil hardness	Coastal sand dunes and grasslands	27, 28
Ctenomyidae	*C. rionegrensis*	Temporal changes in overlap and size of home ranges	Population density (presence of juveniles)	Sand dunes	29
Octodontidae	*Octodon degus*	Spatial variation in home range size	Predation or population density	Mediterranean thorn scrub	30
			Predation, food availability	Scrubland	31
		Temporal changes in home range	Food abundance, quality	Scrubland	32

Family	Species	Aspect of social organization	Ecological correlate	Habitat	Reference
		size			
		Group size	Habitat structure, predation	Scrubland	33
Chinchillidae	*Lagostomus maximus*	Group size	Food abundance, predation	Semiarid scrub	34

Appendix 2: Intraspecific variation in social systems and ecological correlates associated with changes in caviomorph social organization

1) Sachser 1986; 2) Asher et al. 2004; 3) Kraus et al. 2003; 4) Rood 1972; 5) Adrian & Sachser 2011; 6) Taraborelli & Moreno 2009; 7) Taber & Macdonald 1992; 8) Corriale et al. 2013; 9) Macdonald 1981; 10) Herrera & Macdonald 1987; 11) Herrera & Macdonald 1989; 12) Herrera et al. 2011; 13) Schaller & Gransden Crawshaw 1981; 14) Endries & Adler 2005; 15) de Almeida et al. 2013; 16) Silva et al. 2008; 17) Stallings et al. 1994; 18) Beck-King et al. 1999; 19) Jorge & Peres 2005; 20) Silvius & Fragoso 2003; 21) Aliaga-Rossel et al. 2008; 22) Emsens et al. 2013; 23) Busch et al. 1989; 24) Malizia 1988; 25) Pearson et al. 1968; 26) Cutrera et al. 2006; 27) Zenuto et al. 1999b; 28) Cutrera et al. 2010; 29) Tassino et al. 2011; 30) Lagos et al. 1995; 31) Hayes et al. 2007; 32) Quirici et al. 2010; 33) Ebensperger & Wallem 2002; 34) Branch et al. 1993

CHAPTER 3: THE MACROECOLOGY OF SUSTAINABILITY

Published as: Burger, JR, CA Allen, JH Brown, WR Burnside, AD Davidson, TS Fristoe, MJ Hamilton, N Mercado-Silva, JC Nekola, JG Okie, W Zuo. 2012. The macroecology of sustainability. PLoS Biology. 10: e1001345.

Abstract: The discipline of sustainability science has emerged in response to concerns of natural and social scientists, policymakers, and lay people about whether the Earth can continue to support human population growth and economic prosperity. Yet sustainability science has developed largely independent from and with little reference to key ecological principles that govern life on Earth. A macroecological perspective highlights three principles that should be integral to sustainability science: 1) physical conservation laws govern the flows of energy and materials between human systems and the environment, 2) smaller systems are connected by these flows to larger systems in which they are embedded, 3) global constraints ultimately limit flows at smaller scales. Over the past few decades, decreasing per-capita rates of consumption of petroleum, phosphate, agricultural land, fresh water, fish, and wood indicate that the growing human population has surpassed the capacity of the Earth to supply enough of these essential resources to sustain even the current population and level of socioeconomic development.

"Sustainability" has become a key concern of scientists, politicians, and lay people – and for good reason. There is increasing evidence that we have approached, or perhaps even surpassed, the capacity of the planet to support continued human population growth and socioeconomic development [1-3]. Currently, humans are appropriating 20-40% of the Earth's terrestrial primary production [4-6], depleting finite supplies of fossil fuels and minerals, and overharvesting 'renewable' natural resources such as fresh water and marine fisheries [7-10]. In the process, we are producing greenhouse gases and other wastes faster than the environment can assimilate them, altering global climate and landscapes, and drastically reducing biodiversity [2]. Concern about whether current trajectories of human demography and socioeconomic activity can continue in the face of such environmental impacts has led to calls for "sustainability." A seminal event was the Brundtland commission report [11], which defined "sustainable development (as) development that meets the needs of the present without compromising the ability of future generations to meet their own needs."

One result has been the emergence of the discipline of sustainability science. "Sustainability science (is) an emerging field of research dealing with the interactions between natural and social systems, and with how those interactions affect the challenge of sustainability: meeting the needs of present and future generations while substantially reducing poverty and conserving the planet's life support systems" (PNAS: http://www.pnas.org/site/misc/sustainability.shtml version accessed 8 October 2010). It is the subject of numerous books, at least three journals (Sustainability Science [Springer]; Sustainability: Science, Practice, & Policy [ProQuest-CSA]; International Journal of Sustainability Science and Studies [Polo Publishing]), and a special section of the

Proceedings of the National Academy of Sciences of the USA (PNAS). In A Survey of University-Based Sustainability Science Programs conducted in 2007 (http://sustainabilityscience.org/content.html?contentid=1484), the American Association for the Advancement of Science listed 103 academic programs, including 64 in U.S. and Canada, and many more have been established subsequently.

Interestingly, despite the above definition, the majority of sustainability science appears to emphasize social science while largely neglecting natural science. A survey of the published literature from 1980 through November 2010 using the Web of Science reveals striking results. Of the 23,535 published papers that include “sustainability” in the title, abstract, or key words, 48% include “development” or “economics”. In contrast, only 17% include any mention of “ecology” or “ecological”, 12% “energy”, 2% “limits”, and fewer than 1% “thermodynamic” or “steady state”. Any assessment of sustainability is necessarily incomplete without incorporating these concepts from the natural sciences.

Human macroecology

A macroecological approach to sustainability aims to understand how humans are integrated into and constrained by the Earth’s systems [12]. In just the last 50,000 years, *Homo sapiens* has expanded out of Africa to become the most dominant species the Earth has ever experienced. Near-exponential population growth, global colonization, and socioeconomic development have been fueled by extracting resources from the environment and transforming them into people, goods, and services. Hunter-gatherers had subsistence economies based on harvesting local biological resources for food and fiber and on burning wood and dung to supplement energy from human metabolism. With the transition to agricultural societies after the last ice age [13] and then to industrial societies within the last two centuries, per capita energy use has increased from approximately 120 watts of human biological metabolism to over 10,000 watts, mostly from fossil fuels [3,14]. Modern economies rely on global networks of extraction, trade, and communication to rapidly distribute vast quantities of energy, materials, and information.

The capacity of the environment to support the requirements of contemporary human societies is not just a matter of political and economic concern. It is also a central aspect of ecology – the study of the interactions between organisms, including humans, and their environments. These relationships always involve exchanges of energy, matter, or information. The scientific principles that govern the flows and transformations of these commodities are fundamental to ecology and directly relevant to sustainability and to the maintenance of ecosystem services, especially in times of energy scarcity [15]. A macroecological perspective highlights three principles that should be combined with perspectives from the social sciences to achieve an integrated science of sustainability.

Principle 1: Thermodynamics & the zero-sum game

The laws of thermodynamics and conservation of energy, mass, and chemical stoichiometry are universal and without exception. These principles are fundamental to biology and ecology [16-18]. They also apply equally to humans and their activities at all spatial and temporal scales. The laws of thermodynamics mean that continual flows and transformations of energy are required to maintain highly organized, far-from-equilibrium states of complex systems, including human societies. For example, increased rates of energy use are required to fuel economic growth and development, raising formidable challenges in a time of growing energy scarcity and insecurity [3,15, 19]. Conservation of mass and stoichiometry means that the planetary quantities of chemical elements are effectively finite [15,18].

Human use of material resources, such as nitrogen and phosphorus, alters flows and affects the distribution and local concentrations in the environment [18]. This is illustrated by the Bristol Bay salmon fishery, which is frequently cited as a success story in sustainable fisheries management [20,21]. In three years for which good data are available (2007-2009) about 70% of the annual wild salmon run was harvested commercially, with one species, sockeye, accounting for about 95% of the catch [22]. From a management perspective, the Bristol Bay sockeye fishery has been sustainable, because annual runs have not declined. Additional implications for sustainability, however, come from considering the effect of human harvest on the flows of energy and materials in the upstream ecosystem (Figure 1). When humans take about 70% of Bristol Bay sockeye runs as commercial catch, this means a 70% reduction in the number of mature salmon returning to their native waters to spawn and complete their life cycles. It also means a concomitant reduction in the supply of salmon to support populations of predators, such as grizzly bears, bald eagles, and indigenous people, all of which historically relied on salmon for a large proportion of their diet [23,24]. Additionally, a 70% harvest means annual removal of more than 83,000 metric tonnes of salmon biomass, consisting of approximately 12,000, 2,500, and 330 tonnes of carbon, nitrogen, and phosphorus, respectively (see supplementary data for sources and calculations). These marine-derived materials are no longer deposited inland in the Bristol Bay watershed, where they once provided important nutrient subsidies to stream, lake, riparian, and terrestrial ecosystems [24-27]. So, for example, one apparent consequence is that net primary production in one oligotrophic lake in the Bristol Bay watershed has decreased “to about 1/3 of its level before commercial fishing” [28]. Seventy percent of Bristol Bay salmon biomass and nutrients are now exported to eastern Asia, western Europe, and the continental U.S., which are the primary markets for commercially harvested wild Alaskan salmon. Our macroecological assessment of the Bristol Bay fishery suggests that “sustainable harvest” of the focal salmon species does not consider the indirect impacts of human take on critical resource flows in the ecosystem (Figure 1). So the Bristol Bay salmon fishery is probably not entirely sustainable even at the “local” scale.

Principle 2: Scale and embeddedness

Most published examples of sustainability focus on maintaining or improving environmental conditions or quality of life in a localized human system, such as a farm, village, city, industry, or country [29,30, and articles following 31]. These socioeconomic systems are not closed or isolated, but instead are open, interconnected, and embedded in larger environmental systems. Human economies extract energy and material resources from the environment and transform them into goods and services. In the process, they create waste products that are released back into the environment. The laws of conservation and thermodynamics mean that the embedded human systems are absolutely dependent on these flows: population growth and economic development require increased rates of consumption of energy and materials and increased production of wastes. The degree of dependence is a function of the size of the economy and its level of socioeconomic development [3]. Most organic farms import fuel, tools, machinery, social services, and even fertilizer, and export their products to markets. A small village in a developing country harvests food, water, and fuel from the surrounding landscape.

Large, complex human systems, such as corporations, cities, and countries, are even more dependent on exchanges with the broader environment and consequently pose formidable challenges for sustainability. Modern cities and nation states are embedded in the global economy, and supported by trade and communication networks that transport people, other organisms, energy, materials, and information. High densities of people and concentrations of socioeconomic activities require massive inputs of energy and materials and produce proportionately large amounts of wastes. Claims that such systems are "sustainable" usually only mean that they are comparatively "green"—that they aim to minimize environmental impacts while offering their inhabitants happy, healthy lifestyles.

A macroecological perspective on the sustainability of local systems emphasizes their interrelations with the larger systems in which they are embedded, rather than viewing these systems in isolation. Portland, Oregon offers an illuminating example. The city of Portland and surrounding Multnomah County, with a population of 715,000 and a median per capita income of $51,000 USD, bills itself and is often hailed by the media as "the most sustainable city in America" (e.g., Sustainlane.com 2008). On the one hand, there can be little question that Portland is relatively green and offers its citizens a pleasant, healthy lifestyle, with exemplary bike paths, parks, gardens, farmers' markets, and recycling programs. About 8% of its electricity comes from renewable non-hydroelectric sources (http://apps3.eere.energy.gov/greenpower/resources/tables/topten.shtml). On the other hand, there also can be no question that Portland is embedded in and completely dependent on environments and economies at regional, national, and global scales (Figure 2). A compilation and quantitative analysis of the flows into and out of the city are informative (see supplementary data for sources and calculations). Each year the Portland metropolitan area consumes at least 1.25 billion liters of gasoline, 28.8 billion megajoules of natural gas, 31.1 billion megajoules of electricity, 136 billion liters of water, and 0.5 million tonnes of food, and the city releases 8.5 million tonnes of carbon as CO_2, 99 billion liters of liquid sewage, and 1 million tonnes of solid waste into the environment. Total domestic and international trade amounts to 24 million tonnes of materials annually. With respect to these flows, Portland is not conspicuously "green"; the above figures are about average for a U.S. city of comparable size [e.g., 32].

A good way to see the embedding problem is to imagine the consequences of cutting off all flows in and out, as military sieges of European castles and cities attempted to do in the Middle Ages. From this point of view and on the short term of days to months, some farms and ranches would be reasonably sustainable, but the residents of a large city or an apartment building would rapidly succumb to thirst, starvation, or disease. Viewed from this perspective, even though Portland may be the greenest and by some definitions "the most sustainable city in America", it is definitely not self-sustaining. Massive flows of energy and materials across the city's boundaries are required just to keep its residents alive, let alone provide them with the lifestyles to which they have become accustomed. Any complete ecological assessment of the sustainability of a local system should consider its connectedness with and dependence on the larger systems in which it is embedded.

Principle 3: global constraints

For thousands of years, humans have harvested fish, other animals, and plants with varying degrees of "sustainability" and lived in settlements that depend on imports and exports of energy and materials. Throughout history, humans have relied on the environment for goods and services and used trade to compensate for imbalances between extraction, production, and consumption at local to regional scales. What is different now are the enormous magnitudes and global scales of the fluxes of energy and materials into and out of human systems. Every year fisheries export thousands of metric tonnes of salmon biomass and the contained energy and nutrients from the Bristol Bay ecosystem to consumers in Asia, Europe, and the U.S. Every year Portland imports ever larger quantities of energy and materials to support its lifestyle and economy. Collectively, such activities, replicated thousands of times across the globe, are transforming the biosphere.

Can the Earth support even current levels of human resource use and waste production, let alone provide for projected population growth and economic development? From our perspective, this should be the critical issue for sustainability science. The emphasis on local and regional scales – as seen in the majority of the sustainability literature and the above two examples – is largely irrelevant if the human demand for essential energy and materials exceeds the capacity of the Earth to supply these resources and if the release of wastes exceeds the capacity of the biosphere to absorb or detoxify these substances.

Human-caused climate change is an obvious and timely case in point. Carbon dioxide has always been a waste product of human metabolism—not only the biological metabolism that consumes oxygen and produces carbon dioxide as it converts food into usable energy for biological activities, but also the extra-biological metabolism that also produces CO_2 as it burns biofuels and fossil fuels to power the maintenance and development of hunter-gatherer, agricultural, and industrial-technological societies. Only in the last century or so, however, has the increasing production of CO_2 by humans overwhelmed the Earth's capacity to absorb it, increasing atmospheric concentrations and warming the planet more each decade. So, for example, efforts to achieve a "sustainable" local economy for a coastal fishing village in a developing country will be overwhelmed if, in only a few decades, a rising sea level caused by global climate change inundates the community. This shows the importance of analyzing sustainability on a global as well as a local and regional scale.

A macroecological approach to sustainability science emphasizes how human socioeconomic systems at any scale depend on the flows of essential energy and material resources at the scale of the biosphere as a whole. The finite Earth system imposes absolute limits on the ecological processes and human activities embedded within it. The impossibility of continued exponential growth of population and resource use in a finite world has long been recognized [33-35]. But repeated failures to reach the limits in the predicted time frames have caused much of the economic establishment and general public to discredit or at least discount Malthusian dynamics. Now, however, there is increasing evidence that humans are pushing if not exceeding global limits [2,3,36,37]. For example, the Footprint Network estimates that the ecological footprint, the amount of land required to maintain the human population at a steady state [9] had exceeded the available land area by more than 50% by 2007 and the imbalance is increasing (http://www.footprintnetwork.org/en/index.php/GFN).

Here we present additional evidence that humans have approached or surpassed the capacity of the biosphere to provide essential and often non-substitutable natural resources. Figure 3 plots trends in the total and per-capita use of agricultural land, fresh water, fisheries, wood, phosphate, petroleum, copper, and coal, as well as GDP, from 1961 to 2008. Note that only oil, copper, coal, and perhaps fresh water show consistent increases in total consumption. Consumption of the other resources peaked in the 1980s or 1990s and has since declined. Dividing the total use of each resource by the human population gives the per capita rate of resource use, which has decreased conspicuously for all commodities except copper and coal. This means that production of these commodities has not kept pace with population growth. Consumption by the present generation is already "compromising the ability of future generations to meet their own needs." And this does not account for continued population growth, which is projected to increase the global population to 9-10 billion by 2050 and would result in substantial further decreases in per capita consumption.

Figure 3 shows results consistent with other analyses reporting "peak" oil, fresh water, and phosphate, meaning that global stocks of these important resources have been depleted to the point that global consumption will soon decrease if it has not already done so [10,37]. Decreased per capita consumption of essential resources might be taken as an encouraging sign of increased efficiency. But the increase in efficiency is also a response to higher prices as a result of decreasing supply and increasing demand. We have included plots for copper and coal to show that overall production of some more abundant commodities has kept pace with population growth, even though the richest stocks have already been exploited. This is typical in ecology: not all essential resources are equally limiting at any given time. Diminishing supplies of some critical resources, such as oil, phosphorus, arable land, and fresh water, jeopardize the capacity to maintain even the current human population and standard of living.

What are the consequences of these trends? Many economists and sustainability scientists suggest that there is little cause for concern, at least in the short term of years to decades. They give several reasons: i) the finite stocks have not been totally exhausted, just depleted; there are still fish in the sea, and oil, water, phosphate, copper, and coal in the ground, they are just getting harder to find and extract; ii) conservation and substitution can compensate for depletion, allowing economies to grow and provide for increases in population and standard of living; iii) production depends more on the relationship between supply and demand as reflected in price than on absolute availability; and iv) the socioeconomic status of contemporary humans depends not so much on raw materials and conventional goods as on electronic information, service industries, and the traditional economic variables of money, capital, labor, wages, prices, and debt.

There are several reasons to question this optimistic scenario. First, the fact that GDP has so far kept pace with population does not imply that resource production will do likewise. Indeed, we have shown that production of some critical resources is not keeping pace. Second, there is limited or zero scope to substitute for some resources. For most of them, all known substitutes are inferior, scarcer, and more costly. For example, there is no substitute for phosphate, which is an essential requirement of all living things and a major constituent of fertilizer. No other element has the special properties of copper, which is used extensively in electronics. Despite extensive recycling of copper, iron, aluminum, and other metals, there is increasing concern about maintaining supplies as the rich natural ores have been depleted [e.g., 38, but see 39]. Third, several of the critical resources have interacting limiting effects. For example, the roughly constant area of land in cultivation since 1990 indicates that modern agriculture has fed the increasing human population by achieving higher yields per unit area. But such increased yields have required increased inputs of oil for powering machinery, fresh water for irrigation, and phosphate for fertilizer. Similarly, increased use of finite fossil fuels has been required to synthesize nitrogen fertilizers and to maintain supplies of mineral resources, such as copper, nickel, and iron, as the richest ores have been depleted and increased energy is required to extract the remaining stocks. An optimistic scenario would suggest that increased use of coal and renewable energy sources such as solar and wind can substitute for depleted reserves of petroleum, but Figure 3 shows a similar pattern of per capita consumption for coal as for other limiting resources, and the capacity of renewables to substitute for fossil fuels is limited by thermodynamic constraints due to low energy density and economic constraints of low energy and monetary return on investment [41-43]. Fourth, these and similar results [e.g., 3] are starting to illuminate the necessary interdependencies between the energetic and material currencies of ecology and the monetary currencies of economics. The relationship between decreasing supply and increasing demand is causing prices of natural resources to increase as they are depleted, and also causing prices of food to increase as fisheries are overharvested and agriculture requires increasing energy and material subsidies [2,8,43]. The bottom line is that the growing human population and economy are being fed by unsustainable use of finite resources of fossil fuel energy, fertilizers, and arable land and by unsustainable harvests of “renewable resources” such as fish, wood, and fresh water. Furthermore, attaining sustainability is additionally complicated by inevitable yet unpredictable changes in both human socioeconomic conditions and the extrinsic global environment [44]. Sustainability will always be a moving target and there cannot be a single long-term stable solution.

Most sustainability science focuses on efforts to improve standards of living and reduce environmental impacts at local to regional scales. These efforts will ultimately and inevitably fail unless the global system is sustainable. There is increasing evidence that modern humans have already exceeded global limits on population and socioeconomic development, because essential resources are being consumed at unsustainable rates. Attaining sustainability at the global scale will require some combination of two things: a decrease in population and/or a decrease in per capita resource consumption [See also 45]. Neither will be easy to achieve. Whether population and resource use can be reduced sufficiently and in time to avoid socioeconomic collapse and attendant human suffering is an open question.

Critics will point out that our examination of sustainability from a macroecological and natural science perspective conveys a message of “doom and gloom” and does not offer “a way forward”. It is true that humanity is faced with difficult choices, and there are no easy solutions. But the role of science is to understand how the world works, not to tell us what we want to hear. The advances of modern medicine have cured some diseases and improved health, but they have not given us immortality, because fundamental limits on human biology constrain us to a finite lifespan. Similarly, fundamental limits on the flows of energy and materials must ultimately limit the human population and level of socioeconomic development. If civilization in anything like its present form is to persist, it must take account of the finite nature of the biosphere.

Conclusion

If sustainability science is to achieve its stated goals of “dealing with the interactions between natural and social systems” so as to “[meet] the needs of present and future generations while substantially reducing poverty and conserving the planet's life support systems” it must take account of the ecological limits on human systems and the inherently ecological nature of the human enterprise. The human economy depends on flows of energy and materials extracted from the environment and transformed by technology to create goods and services. These flows are governed by physical conservation laws. These flows rarely balance at local or regional scales. More importantly, however, because these systems are all embedded in the global system, the flows of critical resources that currently sustain socioeconomic systems at these scales are jeopardized by unsustainable consumption at the scale of the biosphere. These ecological relationships will determine whether “sustainability” means anything more than “green”, and whether “future generations [will be able] to meet their own needs”.

Acknowledgements

This paper is a product of the Human Macroecology Group, an informal collaboration of scientists associated with the University of New Mexico and the Santa Fe Institute. It benefits from discussions with many colleagues on the important but controversial topic of sustainability. We thank Woody Woodruff, Matthew Moerschbaecher, and John Day for providing helpful comments on the manuscript.

References

1. Goodland, R (1995) The concept of environmental sustainability. Ann Rev Ecol System 26: 1-24.
2. Rockström, J et al. (2009) A safe operating space for humanity. Nature 461: 472-475.
3. Brown, JH et al. (2011) Energetic limits to economic growth. BioScience 61: 19-26.
4. Vitousek, PM, Mooney, HA, Lubchenco, J & Melillo, JM (1997) Human domination of Earth's ecosystems. Science 277: 494-499.
5. Imhoff, ML et al. (2004) Global patterns in human consumption of net primary production. Nature 429: 870-873.
6. Haberl, H et al. (2007) Quantifying and mapping the human appropriation of net primary production in earth's terrestrial ecosystems. Proc Natl Acad Sci U S A 104: 12942-12947.
7. Pauly, D, Watson, R & Alder, J (2005) Global trends in world fisheries: impacts on marine ecosystems and food security. Phil Trans Roy Soc B 360: 5-12.
8. Worm, B et al. (2006) Impacts of biodiversity loss on ocean ecosystem services. Science 314: 787-790.
9. Wackernagel, M & Rees, WE (1996) Our ecological footprint: reducing human impact on the earth. New Society Publications.
10. Gleick, PH & Palaniappan, M (2010) Peak water limits to freshwater withdrawal and use. Proc Natl Acad Sci U S A 107: 11155-11162.
11. Brundtland, GH (1987) World Commission on Environment and Development. Our common future.

12. Burnside, WR et al. (2012) Human macroecology: linking pattern and process in big picture human ecology. Biol Rev. 87:194-2008.

13. Day, JW et al. (2007) Restoration of the Mississippi Delta: lessons from hurricanes Katrina and Rita. Science 315: 1679-1684.

14. Moses, ME & Brown, JH (2003) Allometry of human fertility and energy use. Ecol Let 6: 295-300.

15. Day Jr, JW et al. (2009) Ecology in times of scarcity. BioScience 59: 321-331.

16. Odum, HT (1971) Environment, power and society. New York, USA, Wiley-Interscience.

17. Odum, HT (2007) Environment, power, and society for the twenty-first century: the hierarchy of energy. Columbia University Press.

18. Sterner, RW & Elser, JJ (2002) Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press.

19. Czúcz, B, Gathman, JP & Mcpherson, GUY. (2010) The impending peak and decline of petroleum production: an underestimated challenge for conservation of ecological integrity. Con Biol 24: 948-956.

20. Hilborn, R, Quinn, TP, Schindler, DE & Rogers, DE (2003) Biocomplexity and fisheries sustainability. Proc Natl Acad Sci U S A 100: 6564-6568.

21. Hilborn, R (2006) Salmon-farming impacts on wild salmon. Proc Natl Acad Sci U S A 103: 15277.

22. ADG&F (2010) Alaska Historical Commercial Salmon Catches, 1878–2010. (Alaska Department of Game and Fish, Division of Commercial Fisheries).

23. Coupland, G, Stewart, K & Patton, K (2010) Do you never get tired of salmon? Evidence for extreme salmon specialization at Prince Rupert harbour, British Columbia. J Anthro Arch 29: 189-207.

24. Cederholm, CJ, Kunze, MD, Murota, T & Sibatani (1999) A Pacific salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. Fisheries 24: 6-15.

25. Gende, SM, Edwards, RT, Willson, MF & Wipfli, MS (2002) Pacific salmon in aquatic and terrestrial ecosystems. BioScience 52: 917-928.

26. Naiman, RJ, Bilby, RE, Schindler, DE & Helfield, JM (2002) Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5: 399-417.

27. Schindler, D.E. et al. (2003) Pacific salmon and the ecology of coastal ecosystems. Front Ecol Enviro 1: 31-37.

28. Schindler, DE, Leavitt, PR, Brock, CS, Johnson, SP & Quay, PD (2005) Marine-derived nutrients, commercial fisheries, and production of salmon and lake algae in Alaska. Ecology 86: 3225-3231.

29. International Council for Science (2002) in Science and Technology for Sustainable Development (Int. Council for Science, Paris)

30. Millenium Ecosystem Assessment (2005) Ecosystems and human well-being: synthesis. Island Press.

31. Turner, BL, Lambin, EF & Reenberg, A (2007) The emergence of land change science for global environmental change and sustainability. Proc Natl Acad Sci U S A 104: 20666-20671.

32. Hillman, T & Ramaswami, A (2010) Greenhouse gas emission footprints and energy use benchmarks for eight US cities. Environ Science & Tech 44: 1902-1910.

33. Malthus, TR (1798) An Essay on the Principle of Population. Prometheus.

34. Ehrlich, PR (1968) The population bomb. New York.

35. Meadows, DH (1972) The Limits of Growth. A Report for The Club of Rome.

36. Holdren, JP (2008) Science and technology for sustainable well-being. Science 319: 424-434.

37. Nel, WP & Van Zyl, G (2010) Defining limits: Energy constrained economic growth. Applied Energy 87: 168-177.

38. Gordon, RB, Bertram, M & Graedel, TE (2006) Metal stocks and sustainability. Proc Natl Acad Sci U S A 103:1209-1214.

39. Kesler, SE & Wilkinson, BH (2008) Earth's copper resources estimated from tectonic diffusion of porphyry copper deposits. Geology 36: 255.

40. Fargione, J, Hill, J, Tilman, D, Polasky, S & Hawthorne, P (2008) Land clearing and the biofuel carbon debt. Science 319: 1235-1238.

41. Hall, CA & Day Jr, JW (2009) Revisiting the limits to growth after peak oil. American Scientist 97: 230–237.

42. Smil, V (2008) Energy in nature and society: general energetics of complex systems. Mit Press.

43. The Royal Society (2009) Reaping the benefits: Science and the sustainabile intensification of global agriculture. London: The Royal Society.

44. Milly, PCD et al. (2008) Stationarity is dead: whither water management? Science 319: 573-574.

45. Cohen, J.E. (1996) How many people can the earth support? WW Norton & Company.

46. Foley, J.A. et al. (2011) Solutions for a cultivated planet. Nature. 478: 337-342.

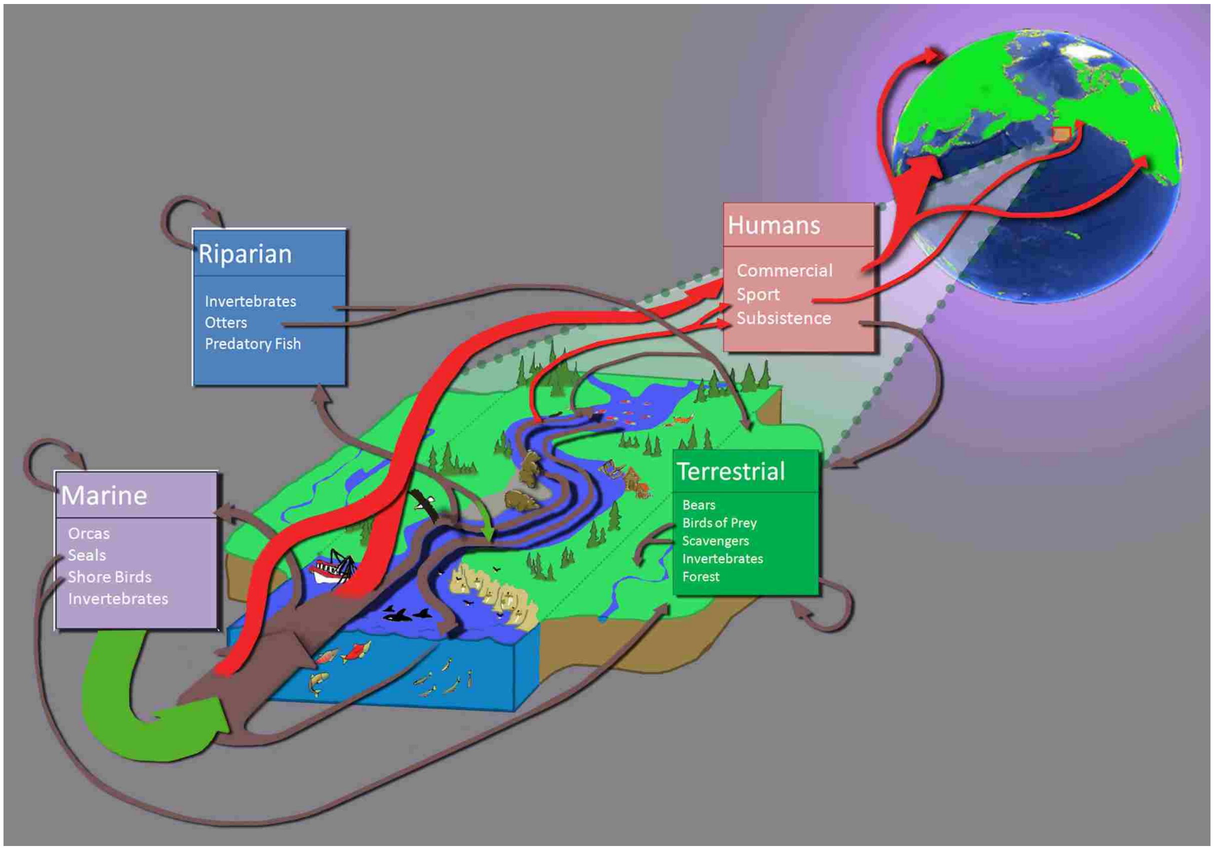


Figure 1. Pictorial illustration of important flows of salmon and contained biomass, energy, and nutrients within and out of the Bristol Bay ecosystem. Brown arrows depict the flows within the ecosystem, green arrows depict inputs due to growth in fresh water or the sea, and red arrows represent human harvest. Seventy percent of salmon are extracted by humans and are no longer available to the Bristol Bay ecosystem. Original art by Trevor Fristoe.

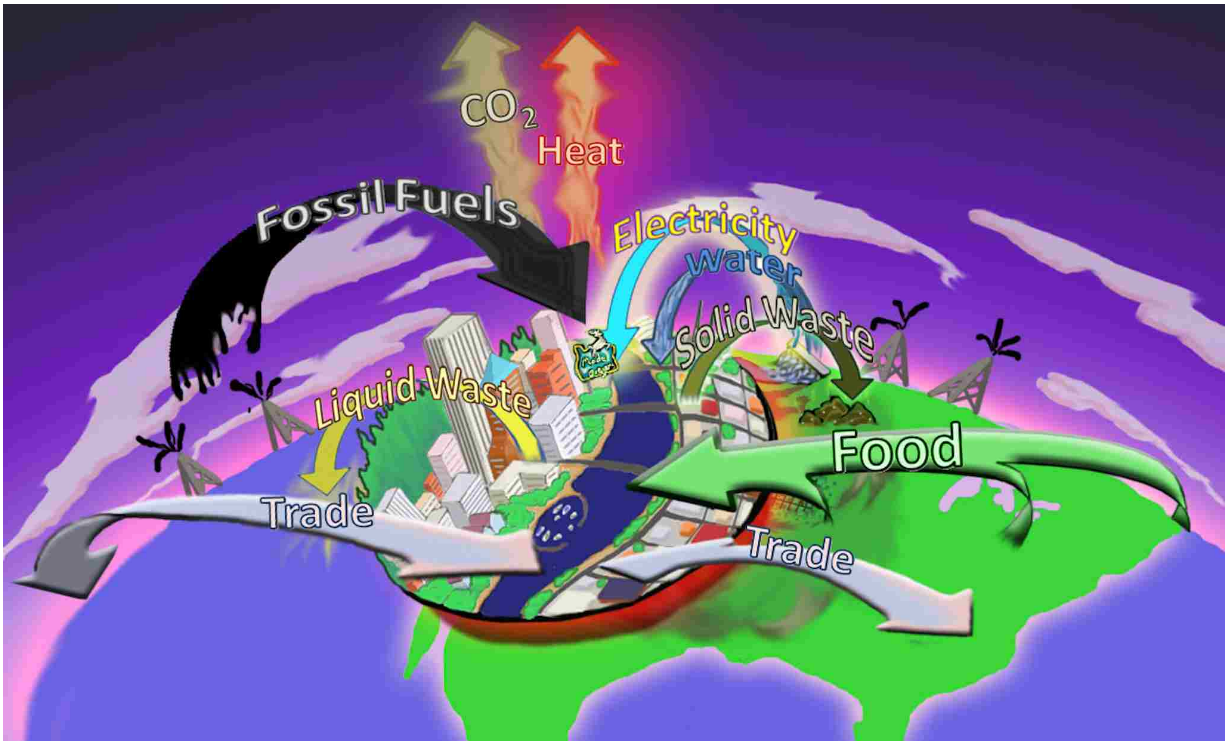


Figure 2. Pictorial illustration of important flows of resources into and wastes out of Portland, Oregon. This "most sustainable city in America" depends on exchanges with the local, regional, and global environments and economies in which it is embedded. Original art by Trevor Fristoe.

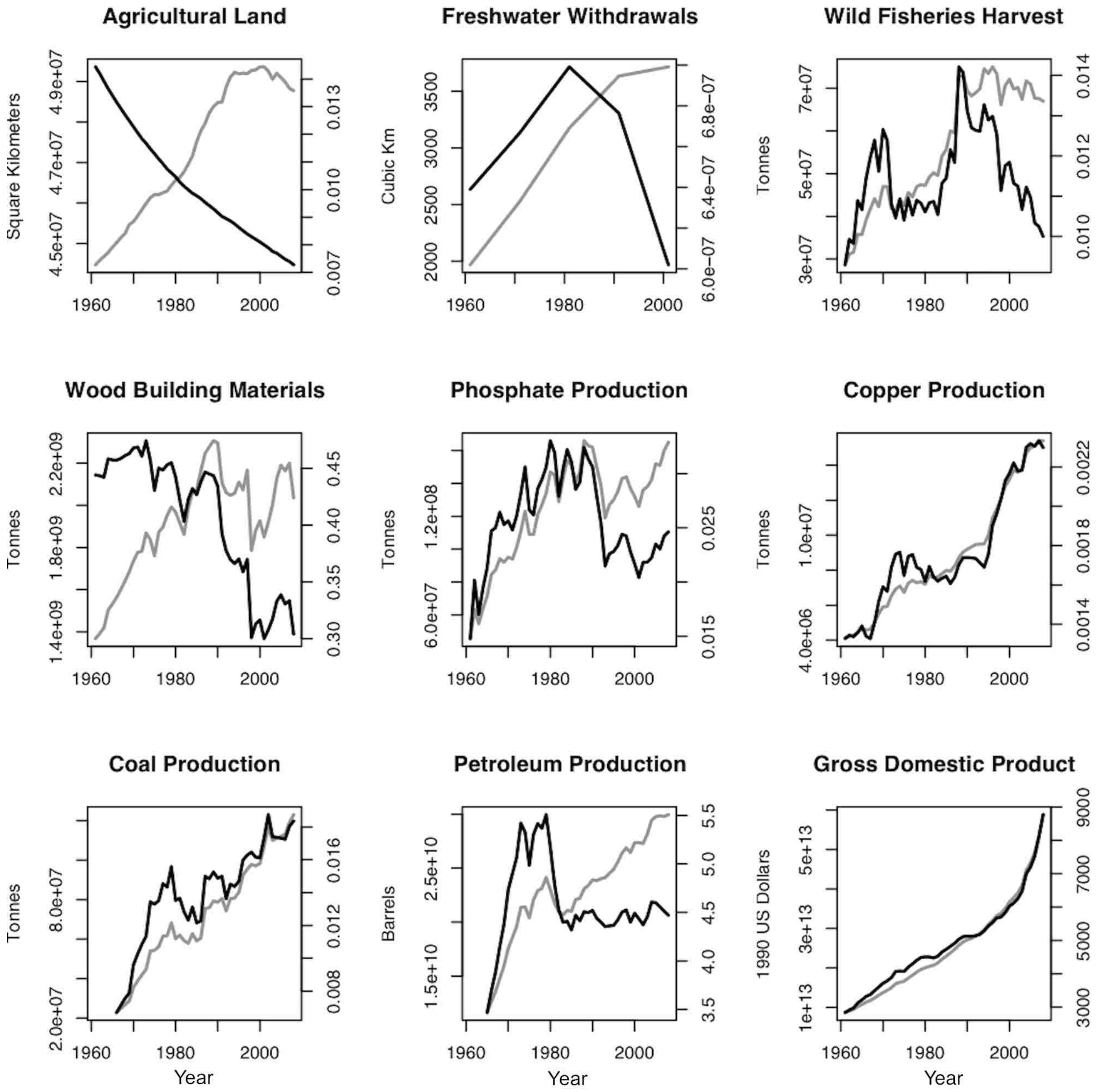


Figure 3. Global trends in total and per capita consumption of resources and GDP from 1961-2008. Total global use/production is represented by the grey line using axis scale on the left side of each diagram. Per capita use/production is represented by the black line using the axis scale on the right side of each diagram. Per capita values represent the total values divided by global population size as reported by the World Resources Institute (http://earthtrends.wri.org/index.php). The Y-axes are untransformed and scaled to allow for maximum dispersion of variance. Individual sources for global use/production values are as

follows: Agricultural land in square-km is from the World Development Indicators Database of the World Bank (http://data.worldbank.org/data-catalog/world-development-indicators) and represents the sum of arable, permanent crop, and permanent pasture lands [see also 46]. Freshwater withdrawal in cubic-km from 1960, 1970, 1980, and 1990 is from UNESCO (http://webworld.unesco.org/water/ihp/db/shiklomanov/ part%273/HTML/Tb_14.html) and for 2000 from The Pacific Insitutute (http://www.worldwater.org/data.html). Wild fisheries harvest in tonnes is from the FAO Fishery Statistical Collection Global Capture Production Database (http://www.fao.org/fishery/statistics/global-capture-production/en) and is limited to diadromous and marine species. Wood building material production in tonnes is based on the FAO ForeSTAT database (http://faostat.fao.org/site/626/default.aspx), and represents the sum of compressed fiberboard, pulpwood+particles (C & NC), chips and particles, hardboard, insulating board, medium density fiberboard, other industrial roundwood (C & NC), particle board, plywood, sawlogs+veneer logs (C & NC), sawnwood (C & NC), veneer sheets, and wood residues. Phosphate, copper, and combustible coal production in tonnes is based on World Production values reported in the USGS Historical Statistics for Mineral and Material Commodities (http://minerals.usgs.gov /ds/2005/140/). Global coal production data is limited to 1966-2008. Petroleum production in barrels from 1965-2008 is based on The Statistical Review of World Energy (http://www.bp.com/sectiongenericarticle800.do?categoryId=9037130&contentId= 7068669) and represents all crude oil, shale oil, and oil sands plus the liquid content of natural gas where this is separately recovered. These data are reported in 1000 barrels/day units, and were transformed to total barrels produced per year. GDP in 1990 US Dollars are from the

World Resources Institute (http://earthtrends.wri.org/index.php). All data were accessed from May 15-June 15, 2011.

Supplemental data

Calculations for salmon nutrient inputs to terrestrial and riparian ecosystems.

We estimated the amount of nitrogen (N), carbon (C), and phosphorous (P) that are removed from natural ecosystems and appropriated by humans due to via wild salmon harvest from Bristol Bay, Alaska. The commercial sockeye harvest in 2010 is estimated to be 83,263 tonnes. This number is based on a capture of 30.5 million individuals at 2.7 kg per fish [1]. Spawning sockeye salmon contain an average 3% fresh wet weight of N, and 0.4% fresh wet weight of P [2]. A 2.7 kg sockeye salmon contains approximately 391.8 g (14% wet weight) of C (calculated from values in [3]). On this basis, in the year 2010 the Bristol Bay fishery exported approximately 2,498 tonnes of N, 333 of P, and 11,881 of C.

Sources of data for the city of Portland and surrounding Multnomah County

Data on:

1) gasoline, natural gas, electricity, water, CO_2, liquid sewage, and garbage from http://www.portlandonline.com (Accessed on 11 October 2010);

2) total domestic and international trade from http://www.aapa ports.org (Accessed on 12 October 2010);

3) food imports estimated based on a population of 715,000, with a metabolic rate of 120W per person consuming the equivalent of 75,161 tonnes of corn per year with energy content of 3.6kJ/g (http://www.nal.usda.gov/fnic/foodcomp/cgi-bin/list_nut_edit.pl. Accessed on 2 December 2010).

References

1. ADF&G (2010) Alaska Historical Commercial Salmon Catches, 1878–2010. (Alaska Department of Game and Fish, Division of Commercial Fisheries).
2. Moore, JW & Schindler, DE (2004) Nutrient export from freshwater ecosystems by anadromous sockeye salmon (*Oncorhynchus nerka*). Can J Fish Aqua Sci 61: 1582-1589.
3. Mathisen, OA et al. (1988) Recycling of marine elements transported into freshwater systems by anadromous salmon. Verh Internat Verein Limnol 23: 2249-2258.

CHAPTER 4: THE CENTRAL ROLE OF ENERGY IN THE GLOBAL URBAN TRANSITION

Authors: Joseph R. Burger, James H. Brown, John W. Day Jr., Tatiana P. Flanagan, Matthew Moerschbaecher, Eric Roy

Affiliations:
Department of Biology, University of New Mexico, 87106 (JRB, JHB, TPF)
Dept. of Oceanography and Coastal Sciences, School of the Coast and Environment, Louisiana State University, 70803 (JWD, MM)
Department of Computer Science, University of New Mexico, 87106 (TPF)
Institute for the Environment and Society, Brown University, 02912 (EDR)
Correspondence e-mail: jrburger@unm.edu

Abstract

The urban transition, the increased ratio of urban to rural population globally and within countries, is a hallmark of the 21st century yet the consequences of this transition for human-natural systems are still debated. We analyze cross-country data spanning several decades from the World Bank to elucidate the patterns and processes that integrate biophysical and socioeconomic systems through urbanization. These include changes in per capita energy use and CO_2 emissions, shifts in resource and non-resource employment, and economic growth. Our analyses reveal that across and within nations over time, per capita Gross Domestic Product (GDP), energy use, and CO_2 production are lowest in predominantly rural countries (rural > urban pop.), increase most rapidly across urbanizing countries (urban ≈ rural pop.) and are highest in the most urban countries (urban > rural pop.). These trends coincide with changes in employment by sector and gender. Rural economies are largely based on male employment in the primary resource-extraction sector, including agriculture, fisheries, and forestry. Urbanizing nations have predominantly male employment in the increasing industry sector, including public utilities. The most urban nations are dominated by service economies, with some countries having up to 90% of female employment in the service sector. These trends that accompany urbanization are likely due to two primary factors as economies transition from rural to urban: i) metabolic energy expended on human and animal labor is increasingly supplemented by extra-metabolic fossil fuel energy to power machines for extracting and transporting raw materials and to support industrial, technological, informational, and service economies predominantly in cities, and ii) energy is used to build and maintain the infrastructure that sustains flows of energy, materials, and information within, into, and out of urban systems. Increasing scarcity of energy and material resources, especially fossil fuels, poses formidable challenges for an urbanizing planet.

Keywords: Biophysical limits; Ecological Economics; Human Macroecology; Non-linear dynamics

Introduction

The unprecedented growth in the modern human economy and population is characterized by feedbacks between resource use, population size, and innovation (Boserup, 1965, Bettencourt et al., 2007, Nekola et al., 2013). A relatively recent trend is the global urban transition where more people now live in cities than rural areas (Fig 1). Developing a science of cities and urbanization is a vibrant area of research that transcends the disciplinary boundaries of the physical, biological, and social sciences. Research into the drivers and consequences of urbanization, and the emergent properties of cities is necessary to disentangle the complex interactions between the socioeconomy and the biophysical environment that will determine the future of the global population and economy.

The increased ratio of urban to rural population and the rapid increase in the number of large cities are often considered encouraging signs that the human population and economy are on a path toward global sustainability. The underlying premise is that concentration of the Earth's growing population and industrial-technological-informational economy in urban centers moderates human impacts on the environment and makes for more efficient use of the planet's limited space and natural resources (Newman, 2006, Jenks and Burgess, 2000). Recent research on scaling of relevant variables with city size has revealed: 1) increasing returns in wealth creation and innovation, including research, development, and 'supercreative' activities, attributed to social interactions facilitated by large cities (Bettencourt et al. 2007; Bettencourt and West 2011; Bettencourt 2013); and 2) economies in space use and infrastructure (Bettencourt et al. 2007), due to high-density housing and efficient transport systems for goods, people, and services (Burton 2000; Capello and Camagni, 2000). From this perspective, cities are viewed as a solution towards sustainable populations and economies (Bettencourt and West 2011). This is based on the premise that urbanization can decouple economic growth from environmental impacts by concentrating population and technology in efficient, innovative cities, which are shifting away from resource-based economies and towards service and technology based economies.

A sociometabolic perspective (*sensu* Krausmann et al., 2008; Sieferle et al. 2006) offers an alternative view of the complex relationships between the biophysical environment and human socioeconomic systems. The human population and economy, like all biological systems, require exchanges with the environment – inputs of energy and material resources and outputs of wastes – for growth, development, and maintenance. As societies develop, shifts from agrarian to industrial-technological-service economies are accompanied by increased consumption of energy and materials, especially fossil fuels, to support high population densities, increased societal complexity, and economic productivity (Krausman et al. 2008). We extend this framework by showing how increased energy use not only fuels the growing industrial, technological, and service economies of the cities but also supplements human and animal labor in rural areas, where increases in agricultural, energy, and mineral production are required to sustain growing cities. This perspective further highlights the manifold consequences of population and economic growth at national and global scales.

Here we develop a simplified macroscopic model of the interactions between the biophysical environment and the human socioeconomy that are most relevant to human ecology and urbanization. From this perspective, urbanization and socioeconomic development depend on both the exchanges of resources and wastes with the biophysical environment and the flows of goods and services within the socioeconomy (Krausmann et al. 2008). This occurs at multiple levels of organization and stages of development ranging from subsistence hunter-gatherers to modern societies with industrial-technological-informational economies (Haberl et al. 2011; Fischer-Kowalski et al. 2014). We use this framework to develop and test predictions for how relationships between energetic, demographic, and economic variables change with the urban transition. This allows us to begin to disentangle complex interactions between energy use and employment and to better understand the socioeconomic and biophysical consequences of urbanization.

Predictions

1) Extra-metabolic energy, largely in the form of fossil fuels, is required to supplement animal and human labor (Roy et al. in review) in growing and developing urban economies. Thus, we predict that with increased urbanization, increased per capita resource use is a necessary consequence of the shift in employment from resource extraction sectors to industrial, service, and technology sectors.

2) Higher per capita energy use to sustain non-resource employment will be reflected in higher CO_2 emissions in more urbanized compared to predominantly rural countries.

3) Increasing employment in industrial and service sectors in urbanized countries will be reflected in greater economic productivity (e.g., in higher GDP per capita).

4) Because increased population density and more developed infrastructure networks of urban systems allow for economies of scale (Boserop 1981; Bettencourt et al. 2007), with increasing urbanization the rate of per capita energy use will increase, but less rapidly than per capita GDP, resulting in less per unit of energy input for economic output.

To test these predictions, we compiled and analyzed data on trends in per capita energy use (thousand tons of oil equivolent: KTOE) and CO_2 emissions (Tonnes), resource- to non-resource employment by sector (percentage), and GDP per capita (in constant US$) as a function of urbanization across countries and within countries over time. We analyzed changes in the proportions of resource producing to industrial- and service-sector employment to evaluate how economic demography changes with urbanization. Our analysis highlights how human labor, which dominates employment and fuels much of the work in rural areas, has been hugely supplemented by extra-metabolic energy in the form of fossil fuels. This has allowed rural areas to produce large surpluses in relation to their own needs and to supply the resources, which have fueled rapid population growth and socioeconomic development of cities. It also allows growth of the non-resource extraction sectors of the economy, including industry and service employment, and economic growth as measured by GDP. We apply change-point analysis to identify shifts in model parameters of linear fits in relevant variables along the urban transition.

Methods

Data

We use publically available data from the World Development Indicators (http://data.worldbank.org) to investigate trends in urbanization across nearly all ~200 countries and spanning half a century. We define urbanization as the log10 ratio of rural to urban population within a country and is calculated using World Bank population estimates and urban ratios from the United Nations' World Urbanization Prospects (http://esa.un.org/unpd/wup/).

We use log10 transformed country level data on per capita energy use, CO_2 emissions, Gross Domestic Product (GDP), and energy intensity (defined as per capita energy use divided by per capita GDP) to characterize their relationships with degree of urbanization (log10 rural/urban population). We use GDP because it is available for all countries, spanning decades and is highly correlated with countless measures of economic well-being including the Human Development Index (Brown et al. 2014). Energy use and CO_2 emissions per capita reflect only rates within a country (i.e., fuel combustion) and not necessarily the total energy required to support a country's GDP (Brown et al., 2011). For example, any fuel combusted and the associated CO_2 emissions in Morocco to mine phosphorus to be used as fertilizer in Brazil is attributed to Morocco and not Brazil.

Our goal was to uncover and quantitatively characterize general trends with urbanization across the vast majority of countries and human population. Five outliers were removed from the ~200 countries because of much greater energy use or CO_2 emissions typical of oil producing nations (Moses and Brown 2003; Brown et al. 2011) and/or urban-island nations with extraordinarily high urban populations (Trinidad and Tobago, Kuwait, Qatar, Hong Kong and Macau). Nonetheless, our analysis includes > 99% of the global population.

To investigate the changes in economic sectors along the urban transition, we also analyzed employment data from the World Bank. We defined **resource employment** in a given country as the total number of individuals publically or privately employed in resource-extraction occupations including agriculture, hunting, forestry, and fishing; **Industry employment** was the total number of individuals that work in industrial jobs including mining and quarrying, oil and gas production, manufacturing, construction, and public utilities such as water, electricity, and, gas. **Service employment** was the total number of individuals in a population employed in the service economy including wholesale and retail trade, hotels and restaurants, transportation, storage, communications, finance, insurance, real estate, business services, health care and education, recreation, and community, social, and personal services.

Analysis

We used spline fits to visually characterize the nonlinear trends in dependent variables along the urban transition, across countries and years. The smoothing parameter, λ, balances tradeoffs between fidelity of the data and roughness of the function estimate by penalizing any curvature. As $\lambda \rightarrow \infty$, only linear functions are allowed, since any curvature at all becomes penalized with an infinitely large number. A λ value of 0 (no smoothing) means that the smoothing spline converges to the interpolated spline fitting all data points. We use the default $\lambda = 1$ for Matlab.

We used change-point analysis to determine if and when major transitions along the urban continuum occur in the data. Change-point analysis is a statistical tool to detect differences in data trends. Cumulative sum (CUSUM) is one technique for assessing when a shift has occurred in data. CUSUM calculates the cumulative sum of the differences between individual data values and the mean of the data. If the data show no shift from the mean, the linear plot of these differences will appear relatively flat with no pronounced changes in slope. Additionally, the range (the difference between the highest and lowest points) will be small. A data set with a shift in the mean will show a visible change in in the change-point plot at the data where the transition occurred. We then assign a confidence level to each change-point detected using bootstrapping.

To assess confidence levels for each change-point, we generated null data sets by calculating the CUSUM for 10 random iterations of the data. We generated each random data set by 'shuffling' the data, matching each value of the dependent variable to a random value of the independent variable. For each randomized data set, we generated the corresponding cumulative sum plots, and calculated the ranges for the sums. The percent times that the cumulative sum range for the original data exceeds the cumulative sum range for the randomized data determines the confidence level. If a pronounced change has occurred, the range on the CUSUM plot for the original data will be large and the random sets will not lead to larger ranges, or will do so infrequently.

After calculating a first level change-point for each dependent variable with urbanization, we fit linear models (Ordinary Least Squares) to characterize trends in each subset of the data, before and after the change-points. We compared parameters (slope and intercept) among variables along the urbanization continuum for data subsets before and after change-points.

Results/Discussion

Patterns: changes in GDP, energy use, CO_2 emissions, and employment with urbanization

Supporting our predictions, increased urbanization coincided with higher energy consumption and CO_2 emissions per individual and resulted in higher economic growth (GDP per capita), across countries and within countries over time (Fig. 2). Energy use was lower in countries with predominantly rural populations and near-subsistence economies, per capita GDP. GDP was usually less than 1,000 US $ per year and energy use less than 500 watts, ~ five times the human metabolic rate of about 100 watts. In highly developed countries with predominantly urban populations, per capita GDP and energy expenditure use was much higher. GDP per capita was usually > 50,000 US $ per year and energy use was usually more than 5,000 watts, about 50 times the human metabolic rate (Fig. 2; see also Brown et al., (2011).

Fitting splines to the data revealed dynamical changes with increasing urbanization (Fig. 2,3). Per capita energy use and CO_2 production show a shallow slope with changes in urbanization across the predominantly rural countries, most steeply through the urban transition (~50% urban), and finally a shallow slope in the predominantly urban countries. Although CO_2 emissions per capita showed signs of leveling (shallow slope) off in the most urbanized countries, the absolute per capita amounts of CO_2 emitted was still much greater in urban compared to rural countries. GDP, in contrast, increased with a similar slope across the entire rural-to-urban spectrum, although it was steeper in the most urbanized countries (Fig 3). One change-point across the rural-to-urban gradient was detected for each variable (Table 1) and these occurred around the urban transition. OLS regression models fitted to data before and after the change-point revealed that energy use and CO_2 emissions per capita showed the steepest slope in predominantly rural countries. In contrast, GDP showed a steeper slope in urbanized countries with greater than 50% urban populations (Table 1, Fig. 3). Consistent with our predictions, log energy use/GDP per capita decreased with increased urbanization as depicted by negative slopes, however, there was no difference in slopes (Table 1) before or after the change-point implying that the urban transition has not resulted in gains in urban energy use efficiency (Fig 3).

As predicted, there was also evidence of substantial changes in employment by sector across the urban transition (Fig 4). In the most rural countries, employment was predominately in occupations related to resource extraction, such as agriculture, timber, and fisheries. Industrial employment increased with urbanization across predominantly rural countries, peaked at approximately the urban transition (50% urban) and then declined in the predominantly urban countries. Service employment dominated the most urban countries, accounting for approximately 90% female employment in the most urban nations. The pervasive trend in employment across the rural-to-urban gradient was a decline in the proportion of the population employed in resource sectors and increase in the proportion working in non-resource (i.e., industrial and service) sectors.

Processes: linking urbanization and employment to resources

Our analysis highlights how human labor, which fuels much of the work in rural areas, has been hugely supplemented by burning fossil fuels to produce surplus to sustain growing urban populations. Large increases in extra-metabolic energy have fueled the rapid population growth and economic development of cities. Fossil fuel supplements in the predominantly rural resource sector has fueled the increased per capita productivity of non-resource based economic sectors, including industry and service employment, resulting in increased economic growth.

As societies develop and populations of countries transition from rural to urban, there has been a pervasive trend of increasing per capita energy use, the vast majority of this derived from fossil fuels, to supplement energy from biological metabolism in the form of human and animal labor. In countries with predominantly rural populations and near-subsistence economies, per capita energy expenditure is only a few times more than the human metabolic rate of 100 watts, reflecting the heavy reliance on human and animal labor and the limited use of fossil fuel for electricity and to power machines. In contrast, highly developed countries with predominantly urban populations have per capita energy expenditures typically more than an order of magnitude higher, exceeding 10,000 watts in nations such as the U.S., U.K., Norway, and Germany. CO_2 emissions exhibit similar patterns.

The increase in energy use across the urban transition reflects interrelated socioeconomic changes. In part, it is a consequence of economic growth (as evidence by increases in GDP) and level of development (Poumanyvong and Kaneko; 2010; Brown et al. 2011) and changes in employment that accompany shifts to industrial and service economies. The least developed countries with predominantly rural populations have consistently low rates of energy use. Their economies are largely based on exploitation of natural resource and near-subsistence agriculture for domestic food consumption. By contrast, the most developed countries with predominantly urban populations have high rates of energy use. Their economies depend heavily on fossil fuels to power energy-demanding industries and services, and to build and maintain complex infrastructure networks for transportation and communication. These activities are concentrated in the cities.

The increase in energy use across the urban transition was also in part a consequence of impacts of the cities on rural areas, which may be far away from the built-up areas. Cities are dependent on flows of energy and materials – people, resources, information, and wastes – into, within, and out of urban centers. Cities are not in steady state with their environments; they require extensive complex transportation networks and infrastructures to move and store food, energy, and raw materials that are produced in rural areas and transformed into goods and services in urban centers (Burger et al. 2012; Hammond et al. in press; Roy et al. in review). For example, transportation currently accounts for 25% of CO_2 emissions globally (IEA 2009) and about 30% in the U.S. (http://needtoknow.nas.edu/energy/energy-use/transportation/). Global trade networks facilitate the flow of materials, people, information, and money and the associated regulatory, service, and information industries, but they require energy to maintain and generate economic activity. Currently, 97% of global GDP and ~65% of global employment (Satterthwaite et al., 2010) are due to the industry and service sectors. This further highlights the dependence of service economies in developed countries on energy and machines to supplement less human labor in the resource sector and to maintain economic growth.

The relationship of the above two phenomena associated with the urban transition, namely energy expenditure on modern industrial-technological-informational economic activities and energy expenditure to provide food and shelter for dense populations in cities, are somewhat confounded. On the one hand, developing countries differ in the degree of urbanization. Some, such as Afghanistan, Burundi, and Rwanda are still predominantly rural and have economies based mostly on subsistence agriculture and extraction and export of raw materials. Others, such as Mexico, India, and Bangladesh have been rapidly becoming urbanized as populations have migrated to cities, even though the economic benefits of urbanization are slower to develop. On the other hand, highly urbanized countries differ in the extent to which they are self-sufficient in resource production. Some, such as Singapore, Switzerland, and Japan, import most of their food, raw materials, and energy. Others such as the U.S., Canada, and Australia have well developed extraction sectors despite the concentration of their populations in large cities. They produce food and other raw materials in excess of domestic requirements and export the products of agriculture, fisheries, forestry, and mining.

Furthermore, despite the urban transition and increased service employment, rural populations in urbanized countries are not necessarily employed in resource sectors. For example, fewer than 2% of the population in most developed countries are employed in agriculture even though ~25% of the population lives in rural areas (Satterthwaite et al., 2010). This is possible because modern industrial agriculture of such highly developed countries is very energy intensive. In the U.S, for example, agriculture accounts for about 15% of total energy expenditure (http://www.ers.usda.gov/publications/err-economic-research-report/err94.aspx) and uses about 10 calories from fossil fuels to produce each calorie of food (Aleklett, 2012). Yet, farmers, ranchers, and fishers currently contribute to less than 3% of employment in the U.S. (Vilsack and Clark, 2014).

Our analysis does not capture the changes in international flows of energy and resources in relation to domestic urbanization. The resource inputs that sustain cities are supplied not only by domestic production and internal transportation, but also by international trade. Cities import resources from fields, forests, oceans, wells, and mines far beyond national boundaries. This may explain in part why GDP increases more steeply than energy use or CO_2 emissions across the predominately urban countries (Table 1; Fig 3). The data we use from the World Bank are for energy consumed and CO_2 emitted from within a given country. However, the most urban countries with large economies import resources from abroad that contribute to economic growth and hence to GDP. So, energy and raw materials imported from developing, predominately rural countries subsidizes population and economic growth in developed urban countries, while manufactured goods and services exported from cities in developed countries contribute to the economies of developing countries. To more precisely quantify the flows of goods and services both direct and indirect measures of production and consumption should be included (Jones and Kammen, 2011). These patterns may give insight into the Environmental Kuznets curve (EKC) – the initial increase and then decrease in apparent environmental impact as countries develop (Suri and Chapman, 1998). A substantial fraction of the environmental impacts of the most developed countries may be beyond their borders. A biophysical analysis quantifying the flows of resources and wastes in international commerce across the rural-to-urban spectrum should clarify the factors that determine the scale and shape of the EKC.

Challenges for the future

The global urban transition from resource producers in rural areas, to industrial and service employment in urban systems is fuelled by supplementing extra-metabolic energy in the form of fossil fuels for decreasing human and animal labor. As populations become concentrated in urban centers, they increasingly rely on primary resource sectors in non-urban areas to supply basic necessities such as food, water, and energy to sustain life and raw materials to build and maintain infrastructure, housing and workplaces. This increasing dependence of rapidly growing cities on imported resources poses formidable challenges for sustaining large urban populations and economies in the face of increasingly scarce finite resources, especially energy (Smil, 2008; Brown et al., 2011; 2014; Burger et al., 2012; Hall and Klitgaard, 2012; Rees, 2012; Day et al., 2014). Renewable energy supplies only make up a fraction of total energy used by the modern economy (Brown et al. 2014) and the energy return on energy invested for renewable energy sources is too low to allow substitution for fossil fuel energy (Hall and Day 2009). Our results show empirically the central role of energy in global urbanization and the coinciding transition from resource extraction to industrial and service economies.

All organisms, including humans have an inherent drive to do better for themselves and their offspring (Nekola et al. 2013). The movement to cities is no exception. Just as animals migrate to improve fitness (Fretwell and Lucas 1970), people are driven by a similar biological imperative to migrate from poor to rich areas, and rural areas to urban centers in order to improve the perceived quality of life and opportunities for themselves and their children. Eighty percent of the North American population is currently urban and the UN predicts that by 2050, two-thirds of the world's population will live in cities with greatest urbanization occurring in Asia and Africa (World Urbanization Prospects 2014). There is much optimism that urbanization will greatly reduce poverty and provide new educational and employment opportunities and a better quality of life for billions of people. Indeed, all developed nations are predominantly urban (Satterthwaite et al., 2010). For these predictions to be met, however, increased energy throughput will be required to grow and sustain the modern socio-economy. If CO_2 emissions are to be reduced in order to mitigate climate change, the fuel sources used to power this activity will need to be non-carbon based. These tradeoffs will have to be faced in an increasingly urbanized and resource-limited world.

Cities, especially those in developed countries, provide many benefits in the form of increased standards of living and quality of life, innovations, wealth creation, and well-paying jobs in industrial-technological-service sectors (Bettencourt et al., 2007). However, urban lifestyles also come with great costs. Cities have and will increasingly continue to rely on smaller proportions of rural populations for energy and materials to feed their citizens, provide raw materials to build and maintain infrastructure, and grow their technology and service economies. It remains to be seen whether cities will continue to provide the innovations required to avoid a global collapse (Bettencourt and West, 2011) in a finite world with complex interactions between the human socioeconomy and the biophysical environment.

Acknowledgements

This manuscript benefits greatly from many discussions with members of the Human Macroecology Group, based at UNM. JRB and TPF were supported by Fellowships in the Program in Interdisciplinary Biological and Biomedical Sciences (grant number T32EB009414) from the National Institute of Biomedical Imaging and Bioengineering. JHB thanks the National Science Foundation Macrosystems Biology Grant EF 1065836 for financial support. EDR was supported by a Voss Postdoctoral Fellowship from the Institute for Environment and Society at Brown University.

References

Aleklett, K. (2012). Peeking at peak oil (Springer Science & Business Media).

Bettencourt, L.M., and West, G.B. (2011). Bigger cities do more with less. Sci. Am. *305*, 52–53.

Bettencourt, L.M., Lobo, J., Helbing, D., Kühnert, C., and West, G.B. (2007). Growth, innovation, scaling, and the pace of life in cities. Proc. Natl. Acad. Sci. *104*, 7301–7306.

Boserup, E. (2005). The conditions of agricultural growth: The economics of agrarian change under population pressure (Transaction Publishers).

Brown, J.H., Burnside, W.R., Davidson, A.D., DeLong, J.P., Dunn, W.C., Hamilton, M.J., Mercado-Silva, N., Nekola, J.C., Okie, J.G., and Woodruff, W.H. (2011). Energetic limits to economic growth. BioScience *61*, 19–26.

Brown, J.H., Burger, J.R., Burnside, W.R., Chang, M., Davidson, A.D., Fristoe, T.S., Hamilton, M.J., Hammond, S.T., Kodric-Brown, A., and Mercado-Silva, N. (2014). Macroecology meets macroeconomics: Resource scarcity and global sustainability. Ecol. Eng. *65*, 24–32.

Burger, J.R., Allen, C.D., Brown, J.H., Burnside, W.R., Davidson, A.D., Fristoe, T.S., Hamilton, M.J., Mercado-Silva, N., Nekola, J.C., and Okie, J.G. (2012). The macroecology of sustainability. PLoS Biol. *10*, e1001345.

Day, J.W., Moerschbaecher, M., Pimentel, D., Hall, C., and Yáñez-Arancibia, A. (2014). Sustainability and place: How emerging mega-trends of the 21st century will affect humans and nature at the landscape level. Ecol. Eng. *65*, 33–48.

IEA 2009. Transport, Energy, and CO_2: Moving Towards Sustainability. International Energy Agency Publications, 9, rue de la Fédération, 75739 Paris, France. ISBN: 978-92-64-07316-6.

Fretwell, S. D. & Lucas, H. L., Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical Development. Acta Biotheoretica 19: 16–36.

Hall, C.A., and Day, J.W. (2009). Revisiting the Limits to Growth After Peak Oil In the 1970s a rising world population and the finite resources available to support it were hot topics. Interest faded—but it's time to take another look. Am Sci *97*, 230–237.

Hall, C.A., and Klitgaard, K.A. (2012). Energy return on investment. In Energy and the Wealth of Nations, (Springer), pp. 309–320.

Jenks, M., and Burgess, R. (2000). Compact cities: sustainable urban forms for developing countries (Taylor & Francis).

Jones, C.M., and Kammen, D.M. (2011). Quantifying carbon footprint reduction opportunities for US households and communities. Environ. Sci. Technol. *45*, 4088–4095.

Krausmann, F., Fischer‐Kowalski, M., Schandl, H., and Eisenmenger, N. (2008). The global sociometabolic transition. J. Ind. Ecol. *12*, 637–656.

Nekola, J.C., Allen, C.D., Brown, J.H., Burger, J.R., Davidson, A.D., Fristoe, T.S., Hamilton, M.J., Hammond, S.T., Kodric-Brown, A., and Mercado-Silva, N. (2013). The Malthusian–Darwinian dynamic and the trajectory of civilization. Trends Ecol. Evol. *28*, 127–130.

Newman, P. (2006). The environmental impact of cities. Environ. Urban. *18*, 275–295.

Poumanyvong, P., and Kaneko, S. (2010). Does urbanization lead to less energy use and lower CO 2 emissions? A cross-country analysis. Ecol. Econ. *70*, 434–444.

Rees, W.E. (2012). Cities as dissipative structures: global change and the vulnerability of urban civilization. In Sustainability Science, (Springer), pp. 247–273.

Satterthwaite, D., McGranahan, G., and Tacoli, C. (2010). Urbanization and its implications for food and farming. Philos. Trans. R. Soc. B Biol. Sci. *365*, 2809–2820.

Smil, V. (2008). Energy in nature and society: general energetics of complex systems (MIT press).

Suri, V., and Chapman, D. (1998). Economic growth, trade and energy: implications for the environmental Kuznets curve. Ecol. Econ. *25*, 195–208.

Vilsack T, Clark CZF (2014). eds. 2014. 2012 Census of Agriculture. Geographic Area Series. United States Department of Agriculture.

Variable		N	Intercept [CIs]	Slope [CIs]	R-squared	p-value
log Energy Use (KTOE)	**Before CP**	2820	2.96 [2.94, 2.97]	0.72 [0.68, 0.75]	0.3320	< 0.001
	After CP	2389	3.20 [3.17, 3.23]	0.40 [0.35, 0.45]	0.0941	< 0.001
log CO_2 (Tonnes)	**Before CP**	4155	0.14 [0.11, 0.16]	1.22 [1.17, 1.27]	0.3650	< 0.001
	After CP	4119	0.41 [0.39, 0.43]	0.62 [0.57, 0.66]	0.1690	< 0.001
log GDP (Constant US$)	**Before CP**	3974	3.05 [3.02, 3.07]	0.77 [0.72, 0.81]	0.2120	< 0.001
	After CP	3984	3.31 [3.29, 3.34]	0.88 [0.83, 0.92]	0.2650	< 0.001
log Energy Use/ GDP	**Before CP**	1448	-0.26 [-0.29, -0.22]	-0.42[-0.49, -0.34]	0.0716	< 0.001
	After CP	2962	-0.27 [-0.29, -0.25]	-0.35[-0.39, -0.30]	0.0719	< 0.001

Table 1. Summary statistics for linear models before (left) and after (right) the change-point along the urban transition in Fig 3.

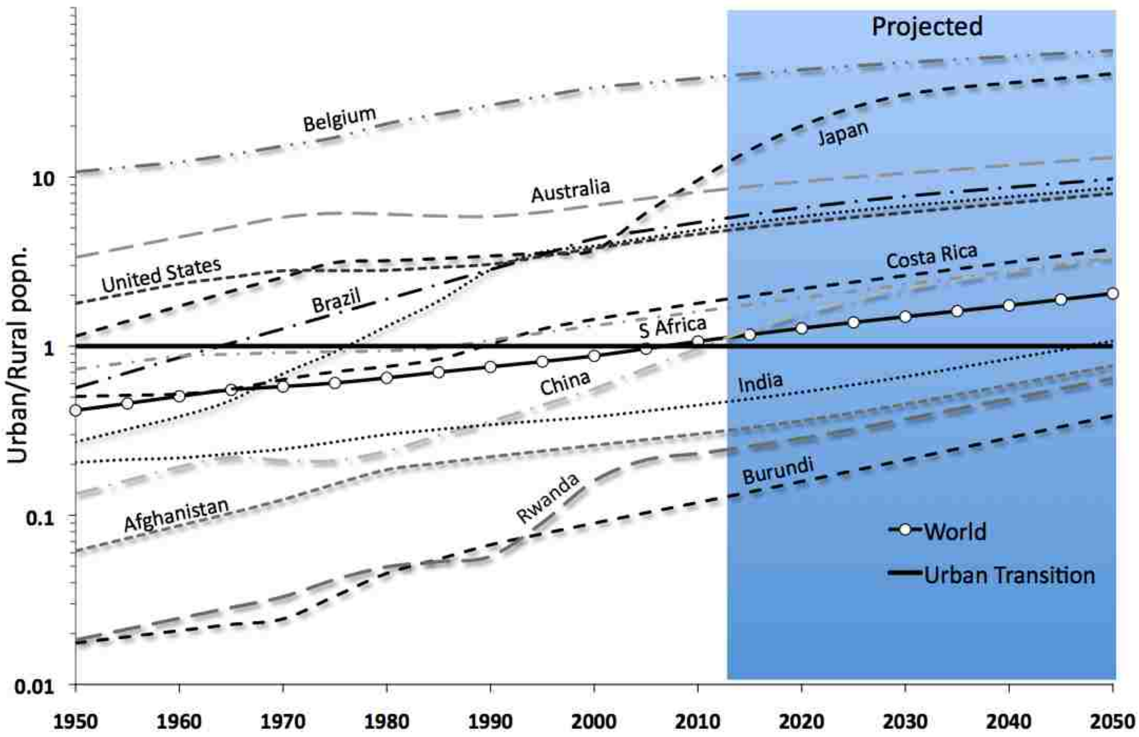


Figure 1: The urban transition globally and for select countries. Data are from the United Nations World Urbanization Prospect (www.esa.un.org) and the World Bank.

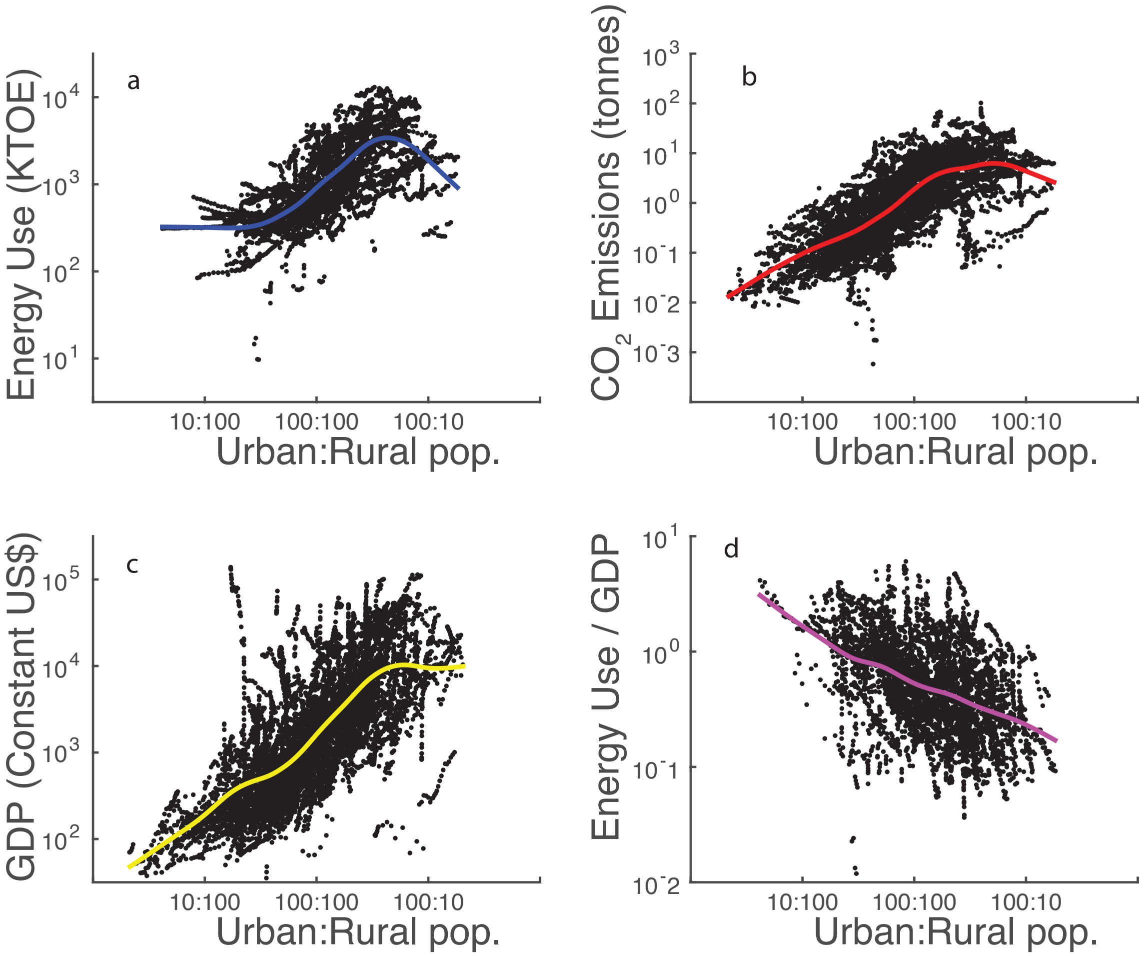


Figure 2: The relationship between log10 per capita energy use (a), CO_2 emissions (b), GDP (c), and energy use/GDP (d) vs log10 urbanization (urban to rural ratio) across years and countries. Colored lines show smooth splines through all points irrespective of country or year.

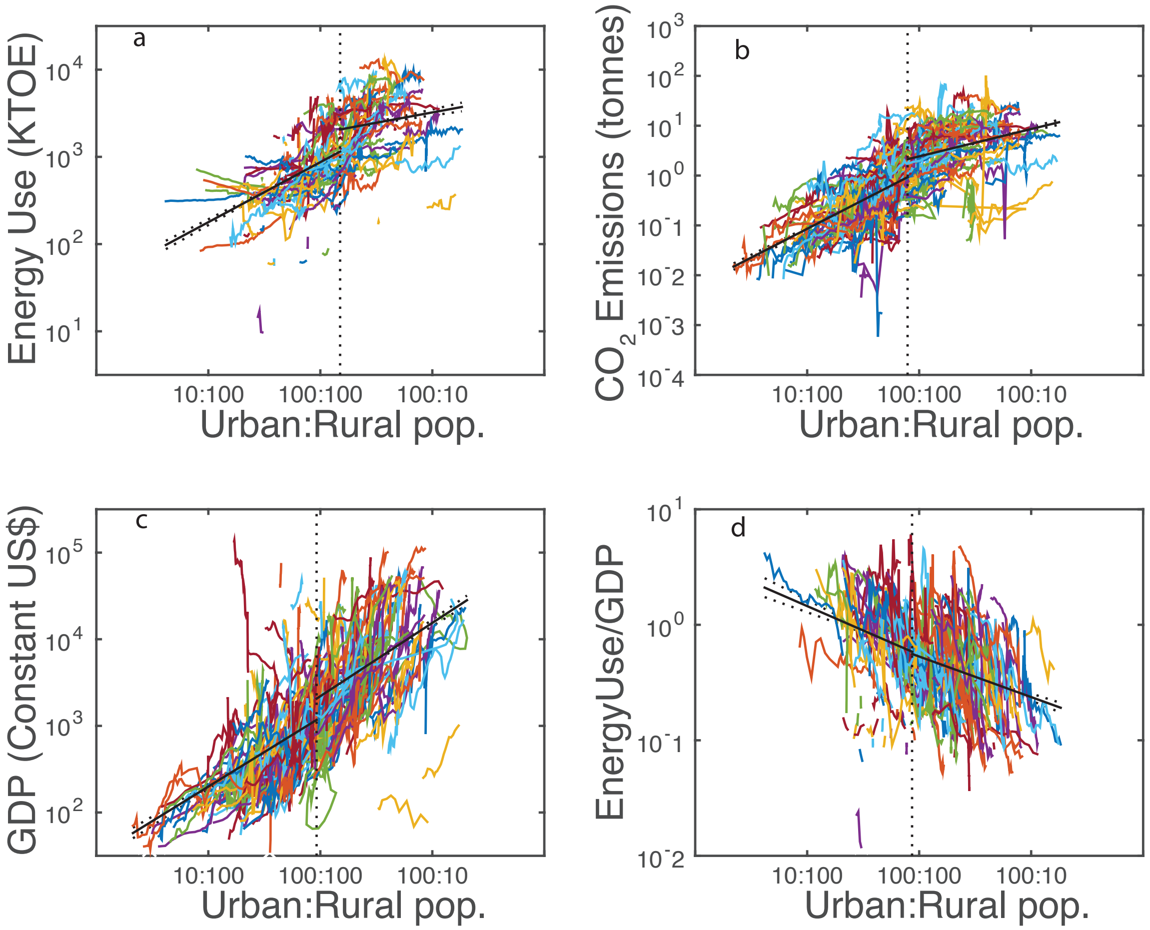


Figure 3: Linear fits (dark lines) to data with confidence intervals (broken lines) before and after change-points (dashed vertical line) for log10 per capita energy use (a), CO_2 emissions (b), GDP (c), and energy use/GDP (d) vs log10 urbanization (urban to rural ratio) across years and countries. Each colored line represents a given country overtime.

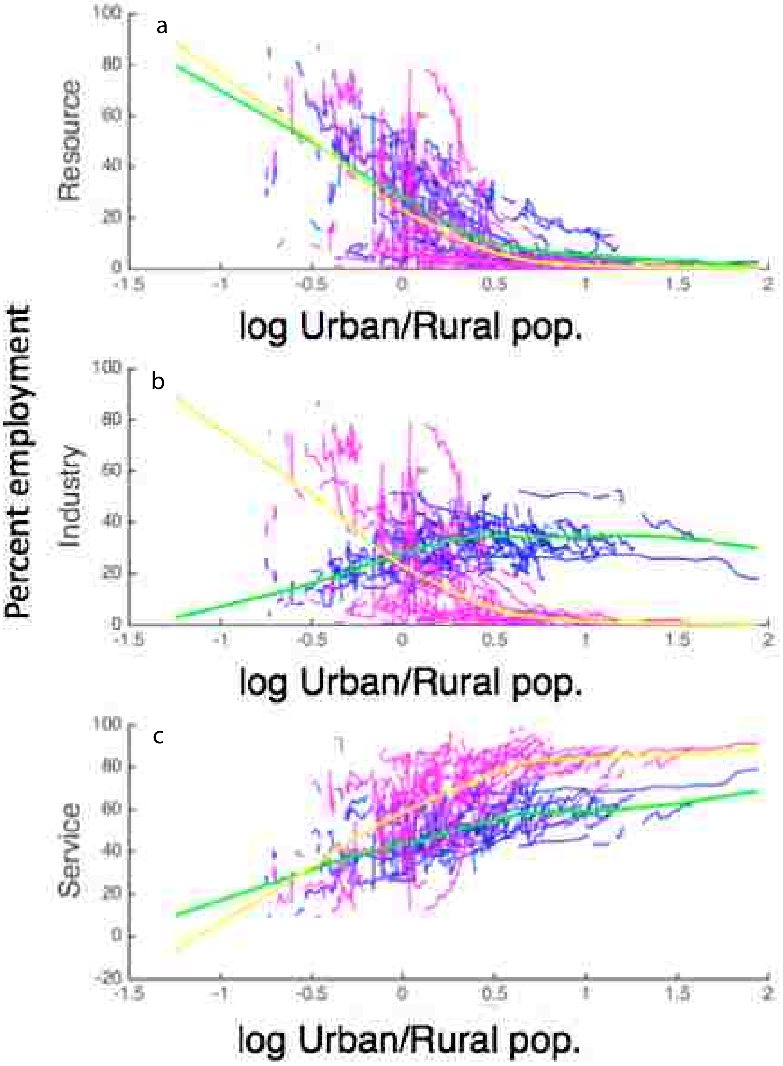


Figure 4: Percent employment in resource (a), industry (b), and service (c) sectors of the economy by gender across the urban transition. Each blue line represents male and pink lines female employment for a given country over time. The green lines are spline fits of all male data and yellow lines are spline fits for all female data.