

**GEOGRAPHIC VARIATION IN TORPOR PATTERNS:
THE NORTHERNMOST PRAIRIE DOGS AND KANGAROO RATS**

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By

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ABSTRACT

Many endotherms use torpor on a seasonal or daily basis to conserve metabolic resources during difficult conditions, but the capacity to do so has never been recognized as varying intraspecifically. I hypothesized that populations that are exposed to prolonged cold, snow, or scarcity of food resources relative to other conspecifics may express torpor despite the fact that other conspecifics may not use, or even be capable of, torpor. I studied thermoregulation of black-tailed prairie dogs (*Cynomys ludovicianus*) and Ord's kangaroo rats (*Dipodomys ordii*) at the extreme northernmost periphery of each species range to determine whether there is evidence for geographic variation in torpor patterns.

Contrary to previous studies of black-tailed prairie dogs near the centre of the species range, I found that northern prairie dogs hibernate during winter, spending up to 95 days per year in torpor. Synchrony of body temperature patterns of some individuals suggests that northern prairie dogs hibernate communally. Similarly, in contrast to previous studies of kangaroo rats in more southern localities, I found that northern Ord's kangaroo rats use daily torpor during winter, entering torpor on up to 70 days per year. Kangaroo rats that use deep torpor exhibit comparable survival and pre-winter body mass, but poorer spring body condition, than kangaroo rats that do not use deep torpor. I reported the details of my procedures for studying thermoregulation of small mammals in the wild, to encourage comparable studies that would provide additional insights on intraspecific variation in torpor patterns. My findings are the first to demonstrate that the capacity for torpor varies predictably on a geographic basis.

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DEDICATION

I dedicate this thesis to my late supervisor, Malcolm Ramsay (1949 – 2000), who died tragically during field research in the arctic, and to my family, who have supported me on so many levels. I am indebted to my wife Krista, daughter Kaitlyn, and son Jack, for their love, support, and patience. I am grateful to my sister-in-law Kelley Kissner and brother-in-law Darren Bender for their personal support and considerable scientific advice. I thank my parents, Beverley and William Gummer, for their love and support, and for instilling my interest in science and nature. I am sad to have lost loved ones much too early in life, my brother Michael Gummer (1976 – 1989) and father-in-law Donald Kissner (1935 – 2004), both of whom would have supported me to the finish and would be happy to see me complete my programme.

TABLE OF CONTENTS

| | |
|--|------|
| PERMISSION TO USE | i |
| ABSTRACT | ii |
| ACKNOWLEDGEMENTS | iii |
| DEDICATION | iv |
| TABLE OF CONTENTS | v |
| LIST OF TABLES | vii |
| LIST OF FIGURES | viii |
| LIST OF ABBREVIATIONS | xii |
| CHAPTER 1. INTRODUCTION | 1 |
| CHAPTER 2. HIBERNATION IN THE NORTHERNMOST BLACK-TAILED PRAIRIE DOGS (<i>CYNOMYS LUDOVICIANUS</i>) | 10 |
| Introduction | 10 |
| Methods | 13 |
| Results | 19 |
| Discussion | 37 |
| Conclusion | 45 |
| CHAPTER 3. WINTER TORPOR IN THE NORTHERNMOST ORD'S KANGAROO RATS (<i>DIPODOMYS ORDII</i>) | 46 |
| Introduction | 46 |
| Methods | 50 |
| Results | 59 |
| Discussion | 68 |
| Conclusion | 83 |
| CHAPTER 4. RELATIONSHIPS BETWEEN TORPOR, SURVIVAL, AND BODY CONDITION OF NORTHERN ORD'S KANGAROO RATS | 85 |
| Introduction | 85 |
| Methods | 90 |
| Results | 94 |
| Discussion | 100 |
| Conclusion | 107 |

| | |
|--|-----|
| CHAPTER 5. MONITORING THERMOREGULATION OF SMALL MAMMALS IN THE WILD | 109 |
| Introduction | 109 |
| Methods | 112 |
| Animal captures | 112 |
| Dataloggers | 113 |
| Anesthesia and surgical procedure | 115 |
| Statistical analyses | 117 |
| Results | 118 |
| Discussion | 120 |
| CHAPTER 6. SYNTHESIS | 125 |
| Major findings | 125 |
| Implications and future directions | 126 |
| REFERENCES | 135 |
| APPENDIX A. IMPORTANCE OF PERIPHERAL POPULATIONS | 153 |
| Abstract | 153 |
| Introduction | 154 |
| General patterns of distribution and abundance | 159 |
| Distribution of geographic range size | 159 |
| Relationship between range size and abundance | 162 |
| Relationship between range size and body size | 164 |
| Intraspecific distribution of abundance | 166 |
| What makes a population peripheral? | 169 |
| Redefining peripheral populations | 176 |
| An empirical evaluation of peripherality | 184 |
| Discussion | 185 |
| Theory of persistence of peripheral populations | 190 |
| Summary | 196 |
| References | 198 |
| APPENDIX B. CLIMATOLOGICAL MAPS OF THE GEOGRAPHIC RANGES OF BLACK-TAILED PRAIRIE DOGS (<i>CYNOMYS LUDOVICIANUS</i>) AND ORD'S KANGAROO RATS (<i>DIPODOMYS ORDII</i>) | 206 |

LIST OF TABLES

| | |
|---|-----|
| Table 2.1 Details of hibernation in 11 free-living black-tailed prairie dogs that were implanted with temperature dataloggers at the northernmost periphery of the species geographic range..... | 22 |
| Table 2.2 Details of daily torpor in 11 free-living black-tailed prairie dogs that were implanted with temperature dataloggers at the northernmost periphery of the species geographic range..... | 23 |
| Table 2.3 Cumulative duration of hibernation and daily torpor among 11 free-living black-tailed prairie dogs that were implanted with temperature dataloggers at the northernmost periphery of the species geographic range..... | 24 |
| Table 2.4 Regression results for fitting a first-order autoregressive quadratic function to describe the seasonal trend of depth of torpor during hibernation among 11 free-living black-tailed prairie dogs that were implanted with temperature dataloggers at the northernmost periphery of the species geographic range..... | 28 |
| Table 2.5 Regression results for fitting a first-order autoregressive quadratic function, and in one case a linear function, to describe the seasonal trend of torpor duration during hibernation among 11 free-living black-tailed prairie dogs that were implanted with temperature dataloggers at the northernmost periphery of the species geographic range..... | 31 |
| Table 2.6 Cross-sectional time series analysis results of separate models relating daily minimum air temperature and snow depth to probability of torpor among 11 free-living black-tailed prairie dogs..... | 35 |
| Table 3.1 Details of winter torpor in two free-living Ord's kangaroo rats at the northernmost periphery of the species geographic range..... | 63 |
| Table 4.1 Details of winter thermoregulation and over-winter survival of 28 radio-collared kangaroo rats at the northernmost periphery of the species geographic range..... | 97 |
| Table A.1 Geographic range metrics of 21 extant species of kangaroo rats..... | 161 |
| Table A.2 Numbers of randomly generated locations that were assigned to the peripheries of distributions of kangaroo rats according to five different methods of estimating peripherality: the median edge-distance model (Median D_E), half edge-distance model (Half D_E), 25 th percentile edge-distance model (25 % D_E), 25 th percentile centre-distance model (25 % D_C), and 25 th percentile weighted-distance model (25 % D_W)..... | 188 |

LIST OF FIGURES

| | |
|--|----|
| Figure 1.1 Geographic range of black-tailed prairie dogs (<i>Cynomys ludovicianus</i>) in southwestern North America (after Hall 1981) with the location of my prairie dog study area indicated by a solid square symbol. | 6 |
| Figure 1.2 Geographic range of Ord's kangaroo rats (<i>Dipodomys ordii</i>) in southwestern North America (after Hall 1981) with the location of my kangaroo rat study area indicated by a solid square symbol. | 7 |
| Figure 2.1 Thermoregulation profiles of seven free-living black-tailed prairie dogs during winter 1999/2000. | 20 |
| Figure 2.2 Thermoregulation profiles of five free-living black-tailed prairie dogs during winter 2000/2001. | 21 |
| Figure 2.3 Seasonal trends in depth of torpor (minimum T_b) during hibernation among seven free-living black-tailed prairie dogs during winter 1999/2000. | 26 |
| Figure 2.4 Seasonal trends in depth of torpor (minimum T_b) during hibernation among five free-living black-tailed prairie dogs during winter 2000/2001. | 27 |
| Figure 2.5 Seasonal trends in duration of torpor during hibernation among seven free-living black-tailed prairie dogs during winter 1999/2000. | 29 |
| Figure 2.6 Seasonal trends in duration of torpor during hibernation among five free-living black-tailed prairie dogs during winter 2000/2001. | 30 |
| Figure 2.7 The proportion of individuals that used torpor each day among seven free-living black-tailed prairie dogs during winter 1999/2000. | 33 |
| Figure 2.8 The proportion of individuals that used torpor each day among five free-living black-tailed prairie dogs during winter 1999/2000. | 34 |
| Figure 2.9 Thermoregulation during hibernation over a representative period of 10 days for six free-living black-tailed prairie dogs that were monitored in the same colony during winter 1999/2000. | 36 |
| Figure 3.1 Thermoregulation profiles of two free-living Ord's kangaroo rats according to hourly measurements of body temperature (T_b) at the northernmost periphery of the species geographic range. | 60 |
| Figure 3.2 Frequency histograms of hourly measurements of body temperature (T_b) of two free-living Ord's kangaroo rats during winter (November through April) at the northernmost periphery of the species geographic range. | 61 |

| | |
|--|-----|
| Figure 3.3 Thermoregulation profiles of two free-living Ord's kangaroo rats according to hourly measurements of body temperature (T_b) at the northernmost periphery of the species geographic range..... | 62 |
| Figure 3.4 Frequency histograms of hourly measurements of body temperature (T_b) of a free-living, female Ord's kangaroo rat during early winter (1-Nov-2001 to 25-Jan-2002; top graph) and late winter (26-Jan-2002 to 18-Apr-2002; bottom graph). | 65 |
| Figure 3.5 Seasonal trends in depth of torpor (minimum T_b) of two free-living Ord's kangaroo rats at the northernmost periphery of the species geographic range. | 66 |
| Figure 3.6 Seasonal trends in duration of torpor of two free-living Ord's kangaroo rats at the northernmost periphery of the species geographic range..... | 67 |
| Figure 3.7 Binary logistic regression of probability of daily torpor with daily minimum air temperature for two free-living Ord's kangaroo rats at the northernmost periphery of the species geographic range. | 69 |
| Figure 3.8 Binary logistic regression of probability of daily torpor with daily snow depth (log-transformed) for two free-living Ord's kangaroo rats at the northernmost periphery of the species geographic range. | 70 |
| Figure 4.1 Cumulative survival of 45 radio-collared kangaroo rats from 24 July 2001 to 16 January 2002 (top graph), relative to the seasonal distribution of torpor use (middle graph) and daily weather conditions (bottom graph)..... | 95 |
| Figure 4.2 Mean (± 1 standard error) of mid-winter body condition (mid-winter mass minus preceding autumn mass) for northern Ord's kangaroo rats that used torpor during early winter ($n = 6$) and those that were not known to use torpor ($n = 7$). ... | 98 |
| Figure 4.3 Spring body condition (spring mass minus preceding autumn mass) for northern Ord's kangaroo rats that used torpor during early winter ($n = 5$; black circles and solid line) and those that were not known to use torpor ($n = 12$; open circles and dashed line). | 99 |
| Figure 4.4 Mean monthly air temperature and number of days with snow on the ground during my study (July 2001 to April 2002; solid circles) and 30-year climate normals (mean $\pm 95\%$ confidence intervals; open circles with error bars) for the nearest meteorological station to my study area (Medicine Hat Airport, Alberta; Environment Canada National Climate Archive 2004). | 101 |
| Figure A.1 The geographic distribution of kangaroo rats (Heteromyidae: <i>Dipodomys</i>) in southwestern North America (after Hall 1981)..... | 158 |
| Figure A.2 The frequency distribution of geographic range sizes of 21 species of kangaroo rats plotted on a logarithmic scale (abscissa). | 160 |

| | |
|---|-----|
| Figure A.3 Bivariate plot of body size versus total area of geographic range for 10 species of kangaroo rats for which mean adult body masses were available in the literature (after Jones 1985). | 165 |
| Figure A.4 Maps of the distributions of peripheral and central regions for the geographic ranges of four species of kangaroo rats, according to the median edge-distance method (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000b)..... | 172 |
| Figure A.5 Maps of the distributions of peripheral and central regions for the geographic ranges of four species of kangaroo rats, according to the half edge-distance method (Channell and Lomolino 2000a). | 174 |
| Figure A.6 Bivariate plot of the estimated area of periphery according to the half edge-distance method (Channell and Lomolino 2000a) versus the median edge-distance method (Channell and Lomolino 2000b, Lomolino and Channell 1998, Lomolino and Channell 1995), for geographic ranges of 21 species of kangaroo rats. | 175 |
| Figure A.7 Maps of relative peripherality for the geographic ranges of four species of kangaroo rats according to the edge-distance model. | 179 |
| Figure A.8 Maps of relative peripherality for the geographic ranges of four species of kangaroo rats according to the centre-distance model. | 181 |
| Figure A.9 Maps of relative peripherality for the geographic ranges of four species of kangaroo rats according to the weighted-distance model. | 183 |
| Figure A.10 Maps of the distributions of peripheral and central regions for the geographic range of Ord's kangaroo rats according to alternative methods of estimating the peripheries: (i) median edge-distance model; (ii) half edge-distance model; (iii) 25 th percentile edge-distance model; (iv) 25 th percentile centre-distance model; and (v) 25 th percentile weighted-distance model. | 186 |
| Figure A.11 Maps of the distribution of peripheral and central regions for the geographic range of Merriam's kangaroo rats according to alternative methods of estimating the peripheries: (i) median edge-distance model; (ii) half edge-distance model; (iii) 25th percentile edge-distance model; (iv) 25th percentile centre-distance model; and (v) 25th percentile weighted-distance model. | 187 |
| Figure B.1 Map of mean annual temperature for southwestern North America overlaid with the geographic distribution of black-tailed prairie dogs (<i>Cynomys ludovicianus</i>). | 207 |
| Figure B.2 Map of mean annual number of days with snow for southwestern North America overlaid with the geographic distribution of black-tailed prairie dogs (<i>Cynomys ludovicianus</i>). | 208 |

Figure B.3 Map of mean annual temperature for southwestern North America overlaid with the geographic distribution of Ord's kangaroo rats (*Dipodomys ordii*).....209

Figure B.4 Map of mean annual number of days with snow for southwestern North America overlaid with the geographic distribution of Ord's kangaroo rats (*Dipodomys ordii*).....210

LIST OF ABBREVIATIONS

ANOVA analysis of variance

FMR field metabolic rate

MR metabolic rate

T_a ambient temperature

T_{act} active temperature

T_b body temperature

T_{sk} skin temperature

V_{O_2} oxygen consumption

CHAPTER 1. INTRODUCTION

Many endotherms use torpor to conserve metabolic resources during difficult conditions (Lyman et al. 1982). Torpor involves a controlled reduction of the thermoregulatory set point, which results in a drop in body temperature (T_b) and metabolic rate (MR measured as $\dot{V}O_2$), thereby achieving substantial conservation of metabolic resources such as energy and water (Hudson 1978, Lyman et al. 1982, Wang and Wolowyk 1988, Geiser 2004). Arousal from the torpid state is accomplished by shivering and non-shivering thermogenesis, independent of exogenous heat, thus differentiating torpor from hypothermia (Hudson 1978).

Torpor has been observed in a diversity of species from at least nine mammalian and six avian orders (Geiser and Ruf 1995, Geiser 1998). A species' use of torpor is generally categorized as either seasonal hibernation or daily torpor according to the duration of torpor bouts (Geiser and Ruf 1995, Geiser 2004). Seasonal hibernation is characterized by torpor bouts with duration > 24 h whereas daily torpor is defined by maximum torpor bout duration < 24 h. Species that use seasonal hibernation tend to have larger body size, lower minimum T_b , and lower MR compared to species that use only daily torpor (Geiser and Ruf 1995). Yet, even daily torpor confers substantial metabolic savings. Shallow torpor episodes are likely to have significant energetic and ecological importance (Webb et al. 1993, Barclay et al. 2001, Willis and Brigham 2003) because shallow reductions in T_b conserve relatively more energy than reductions of the same increment at lower T_b (Studier 1981).

Intraspecific variation in torpor characteristics has been documented in response to a number of variables, including diet and body condition (Geiser et al. 1997, Florant 1998, Harlow and Frank 2001, Frank 2002, Munro and Thomas 2004), sex and reproductive status (Michener 1992, Hamilton and Barclay 1994, Grinevitch et al. 1995, Mzilikazi et al. 2002), age class (Michener 1992, Armitage et al. 2003), group size (Lynch et al. 1978), ambient conditions (Lynch et al. 1978, Buck and Barnes 1999), and as an artifact of captive breeding (Geiser and Ferguson 2001) or laboratory conditions (Geiser et al. 2000). However, the general capacity to use torpor is not typically considered to vary intraspecifically. Species are generally considered to be capable of torpor or not. Yet ecologists have long recognized that many traits of organisms vary both inter- and intraspecifically on a geographic basis in association with climatic gradients. For example, classical biogeographic rules relate inter- and intraspecific variation in body size and relative size of extremities to latitudinal climate gradients (Bergmann's rule and Allen's rule, respectively; Mayr 1956, Mayr 1963, Endler 1977, Freckleton et al. 2003, Meiri and Dayan 2003). The capability and extent of torpor may similarly vary intraspecifically with geography and climate. Certain populations that are exposed to extreme or prolonged cold, snow, or scarcity of food resources, relative to other conspecifics, may use torpor to facilitate survival despite the fact that other conspecifics may not use, or even be capable of, torpor.

The theory that torpor may be endemic to certain populations of a species is not unjustified. Torpor is already known to occur among such a broad diversity of animals that there is increasing acceptance that endothermic heterothermy is likely to be plesiomorphic (Malan 1996, Geiser 1998, Lovegrove et al. 1999, Grigg and Beard 2000). To assume that endothermic heterothermy arose independently on multiple

occasions would be less parsimonious than to consider it as ancestral (Grigg and Beard 2000). Based on the phylogenetic diversity of animals that use torpor, as well as observations of ectothermic, circadian heterothermy in reptiles, Malan (1996) suggested that euthermic homeostasis, hibernation, and daily torpor evolved from a common pattern of circadian heterothermy, ectothermic at first and later facilitated by endothermic thermogenesis. He advocated that torpor should not be considered as a repetitive independent occurrence of a secondary adaptation, but instead as the recurring expression of ancestral traits (Malan 1996). If endothermic heterothermy is plesiomorphic, then for certain populations to adopt torpor would only necessitate recurrence of expression of existing, ancestral traits, potentially resulting in torpor use varying on a geographic basis across a species range.

If torpor capabilities of some species vary intraspecifically on a geographic basis, those species would be useful study systems for comparative research on the underlying physiological mechanisms of torpor and relative influences of genetic and environmental factors on characteristics and expression of torpor. Confirmation of geographic variation in torpor capabilities would also provide an improved position for modeling energetics, populations, and species ranges, particularly where linkages between energetics and climate are presumed to limit populations or distributions (e.g., Humphries et al. 2002). Additionally, geographic variation in thermoregulation and energetics may represent an important, previously unrecognized component of population diversity (Hughes et al. 1997, Ceballos and Ehrlich 2002) that may contribute to the persistence of some species through periods of change in climate or food availability.

Currently there are only a few examples that provide evidence for potential geographic variation in torpor use. Lyman et al. (1982) reviewed the substantial

variation in use of torpor among white-footed mice (*Peromyscus leucopus*) and speculated that torpor may vary between subspecies that occur in different geographic areas. Grigg and Beard (2000) pointed out that thermoregulation patterns of short-beaked echidnas (*Tachyglossus aculeatus*) appear to vary from torpor being rare in warm regions to all individuals adopting prolonged hibernation in cooler regions. There was also recent confirmation of daily torpor in common nighthawks (*Chordeleis minor*) in one region of the breeding range that imposes particularly cold T_a during summer nights (Fletcher et al. 2004), despite the fact that comparable field studies of other populations of the species in other locales yielded no evidence of torpor (Firman et al. 1993). Fletcher et al. (2004) indicated that the capability of torpor may vary between (breeding) populations that occupy different geographic regions.

Systematic studies of thermoregulation of endothermic animals across species ranges have yet to be conducted; the traditional approach of physiological ecology has been to assume that the characteristics of animals in as few as one or two locales, or even of captive animals under laboratory conditions, are adequately representative of the species. There has been a high reliance of thermoregulation studies on captive animals—from which the real world relevance is frequently not apparent (Geiser et al. 2000). Torpor characteristics can be significantly affected by the particular conditions of captivity (Geiser et al. 2000, Geiser and Ferguson 2001). Field studies of thermoregulation of free-living animals are needed, and are expected to reveal more widespread and intensive use of torpor than previously realized (Geiser et al. 2000). Ultimately, only field studies can determine the importance of torpor for survival and fitness of animals in the wild (Geiser et al. 2000).

Northernmost, peripheral populations of north-temperature endotherms that were previously assumed to be incapable of torpor, based on studies of southern conspecifics, provide an opportunity for research on torpor capabilities and potential geographic variation in thermoregulation and energetics. Typically, northern populations are the most likely members of the species to encounter extreme winter conditions that may necessitate torpor because winter at high latitude simultaneously reduces resource availability and increases resource requirements (King and Murphy 1985, Davenport 1992). Under these conditions, expression of torpor should be favoured in those populations as compared to populations experiencing more moderate variation in climate and food availability.

I studied thermoregulation and torpor of black-tailed prairie dogs (Sciuridae: *Cynomys ludovicianus*) and Ord's kangaroo rats (Heteromyidae: *Dipodomys ordii*) at the extreme northernmost peripheries of the species geographic ranges (Figs. 1.1 and 1.2, respectively) to determine whether there is evidence for geographic variation in thermoregulation and energetics of endotherms. The northernmost populations of these species are peripheral both in terms of proximity to the edge and distance from the centre of the species distribution (Appendix A). They also appear to be geographically isolated from the nearest conspecifics to the south (Gummer 1995, 1997, 1999). Both species have been the subject of extensive physiological and behavioural studies in more southern portions of their ranges (see French 1993, Hoogland 1995, Harlow 1997) and the general belief that these animals do not hibernate or use torpor under natural conditions has contributed to many perspectives and comparative studies in physiological and evolutionary ecology (e.g., Hamilton and Pfeiffer 1977, Armitage 1981, MacMillen 1983, Michener 1983, Michener 1984, French 1993, Harlow and

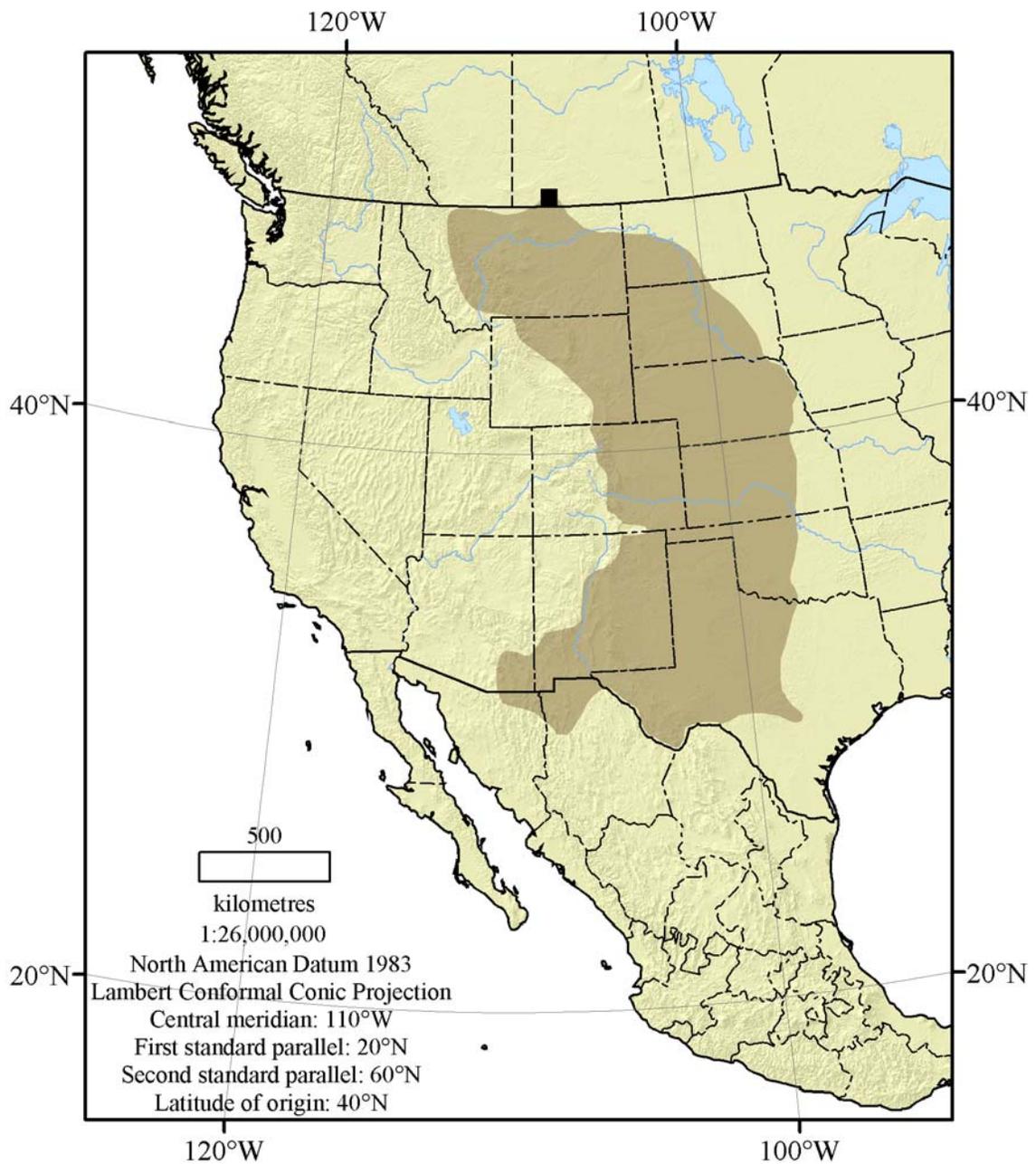


Figure 1.1 Geographic range of black-tailed prairie dogs (*Cynomys ludovicianus*) in southwestern North America (after Hall 1981) with the location of my prairie dog study area indicated by a solid square symbol.

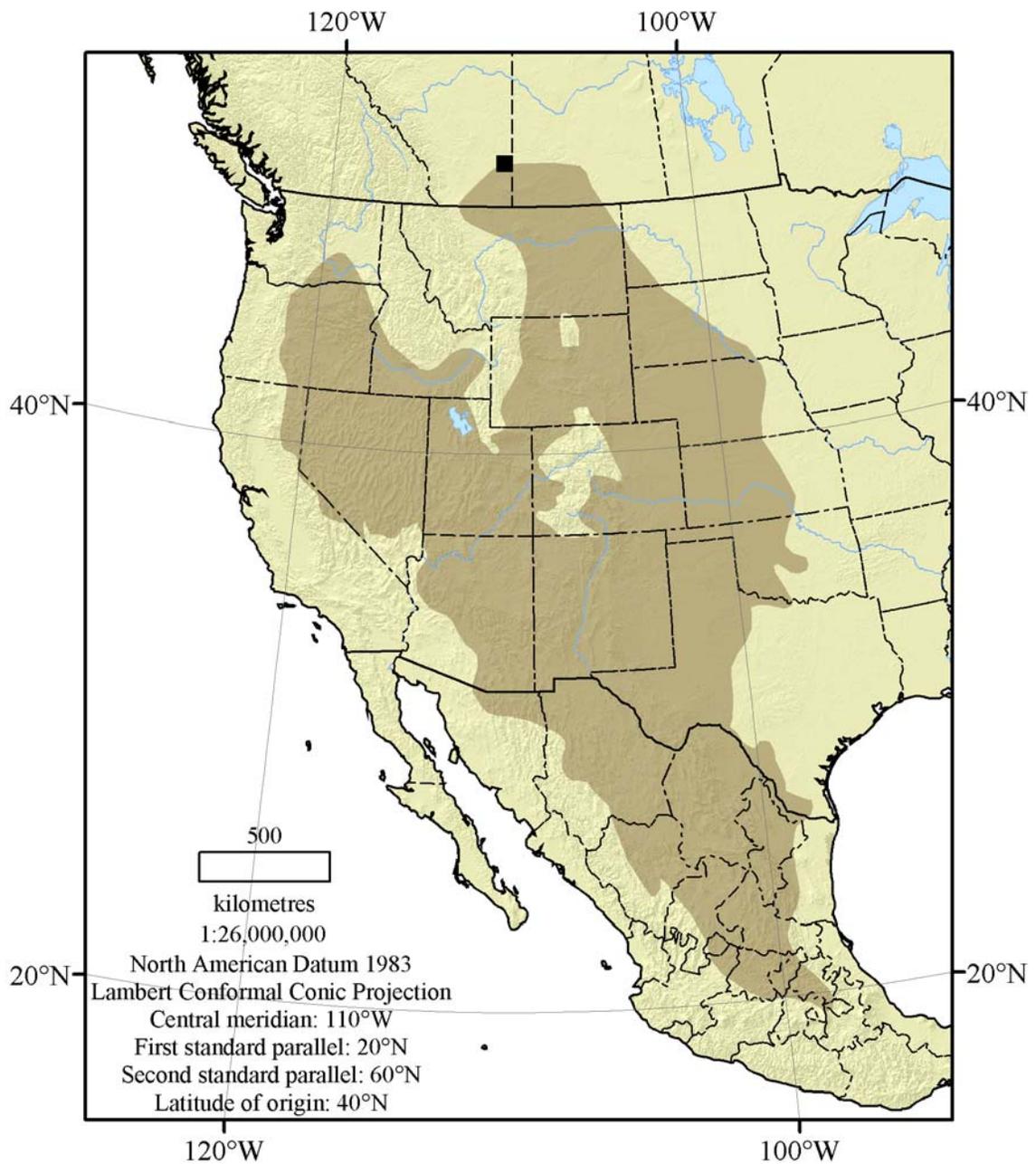


Figure 1.2 Geographic range of Ord's kangaroo rats (*Dipodomys ordii*) in southwestern North America (after Hall 1981) with the location of my kangaroo rat study area indicated by a solid square symbol.

Menkins 1986, Harlow 1995, Hoogland 1995, Harlow 1997, Harlow and Frank 2001, Lehmer and Van Horne 2001). However, northern prairie dogs and kangaroo rats presumably experience relatively harsh winter weather conditions compared to more southern conspecifics, as is suggested by climate maps that illustrate relatively low mean annual temperature and high mean annual number of days with snow compared to the majority of the species geographic ranges (Appendix B). Hence I expected that if any population of each species expresses torpor, it would most likely be the northernmost population.

I present the chapters of my dissertation as independent papers, requiring some minor overlap in background information and methodology among chapters. In Chapter Two I examine whether black-tailed prairie dogs hibernate at the northernmost periphery of the species geographic range by experimentally implanting and recovering temperature dataloggers in wild, free-living prairie dogs. I document patterns of thermoregulation of northern prairie dogs, including the proportion of time in a torpid state, depth and duration of torpor, seasonal trends, and relative synchrony of thermoregulation patterns among prairie dogs. In Chapter Three I investigate the prospect of winter torpor by Ord's kangaroo rats at the northernmost periphery of the species geographic range by experimentally implanting and recovering miniature temperature dataloggers in wild, free-living kangaroo rats. I characterize thermoregulation of northern kangaroo rats according to torpor frequency, depth, duration, and seasonality. In Chapter Four I evaluate relationships between torpor, survival, and body condition of radio-collared kangaroo rats to distinguish thermoregulation patterns of the northern population from those previously reported in captive congeners from more southern localities, and to clarify the potential role of

torpor in over-winter survival of the northernmost population. In Chapter Five I explore a new method for studying thermoregulation of small mammals in the field and I provide details of my procedures for field monitoring of thermoregulation that can be applied to prairie dogs, kangaroo rats, or other small endotherms for investigation of geographic variation in thermoregulation and energetics. In Chapter Six I review my cumulative findings and discuss general implications of my research regarding the hypothesis of geographic variation in patterns of thermoregulation and energetics of endotherms.

CHAPTER 2. HIBERNATION IN THE NORTHERNMOST BLACK-TAILED PRAIRIE DOGS (*CYNOMYS LUDOVICIANUS*)

Introduction

Prairie dogs (*Cynomys*) are diurnal, gregarious herbivores. Of the five extant species of prairie dogs, three species (*C. gunnisoni*, *C. leucurus*, *C. parvidens*) are generally considered hibernators whereas two species (*C. ludovicianus* and *C. mexicanus*) are not considered to hibernate under natural conditions (Bakko 1977, Michener 1983, Bakko et al. 1988, Hoogland 1995, Harlow 1997, Hoogland 1997, Lehmer and Van Horne 2001, Lehmer et al. 2001, Lehmer et al. 2003). The black-tailed prairie dog (*C. ludovicianus*) has the broadest geographic distribution of the prairie dogs and it is the only ground-dwelling sciurid with a geographic range extending north of 40 °N that is not thought to hibernate (Bakko et al. 1988).

Black-tailed prairie dogs are also among the most social of the ground-dwelling sciurids (Armitage 1981, Michener 1983, Michener 1984, Hoogland 1995). Generally, year-round euthermy may facilitate development of social relationships among individuals of different sex and age classes. Michener (1984:98) suggested that, especially for species that hibernate, differences in the temporal distribution of active seasons among age classes “may limit the extent to which complex, integrative bonds develop among individuals of different ages.” In cases where there are adaptive benefits of sociality, species in which all age classes are simultaneously active year-round may

be more likely to develop high levels of sociality compared to species in which there is temporal segregation of age classes. Moreover, year-round euthermy may also be promoted by sociality, because bonds between individuals are likely to be conducive to communal nesting that should minimize heat loss, thereby assisting energy conservation and survival during cold periods.

Black-tailed prairie dogs have not generally been considered to hibernate because they are observed foraging aboveground throughout the year across the majority of the species geographic range (King 1955, Koford 1958, Tileston and Lechleitner 1966, Bakko et al. 1988, Hoogland 1995, Harlow 1997, Hoogland 1997). Laboratory experiments with captive black-tailed prairie dogs collected from localities near the centre of the species geographic range have shown that torpor can be induced in some individuals through severe food and water deprivation at cold temperatures (Anthony 1953, Hamilton and Pfeiffer 1977, Harlow and Menkens 1986, Harlow 1995, Harlow 1997, Harlow and Frank 2001). In addition, at least two field studies examined thermoregulation of wild black-tailed prairie dogs. Bakko et al. (1988) concluded that black-tailed prairie dogs in Colorado did not use torpor during 1976-1977 according to body temperature (T_b) measurements by implanted radio transmitters. In contrast, Lehmer et al. (2001, 2003) recently reported that 12 black-tailed prairie dogs in Colorado used torpor infrequently during 1998-2000 according to T_b measurements by implanted temperature dataloggers. Overall, field and laboratory findings suggest that black-tailed prairie dogs may use shallow, infrequent torpor under extraordinary circumstances, such as food or water deprivation in conjunction with cold ambient temperatures. In no instances have extended, repetitive cycles of deep torpor constituting hibernation been documented in this species. Lehmer and Van Horn (2001:964) found

that lipid deposition and use in black-tailed prairie dogs differed from that typical of hibernators and “may partly explain why black-tailed prairie dogs are unable to undergo the prolonged winter dormancy characteristic of hibernation.”

Despite these laboratory and field observations, it is premature to discount the potential of hibernation among black-tailed prairie dogs based strictly on laboratory and field investigations of prairie dogs from central regions of the species geographic distribution where individuals are exposed to relatively moderate climate. There have been no previous studies of black-tailed prairie dogs near the northernmost periphery of the species geographic range, where the species is likely subjected to the coldest and longest winters of any population in the genus (Appendix B). The 30-year normal January daily minimum air temperature at the nearest meteorological station (Val Marie, Saskatchewan) to the northernmost population of (black-tailed) prairie dogs is $-18.8\text{ }^{\circ}\text{C}$ (Environment Canada National Climate Archive 2004), which is at least $12.6\text{ }^{\circ}\text{C}$ lower than the mean minimum temperature reported for either black-tailed or white-tailed prairie dog colonies in Wyoming and Colorado where animals were collected for previous laboratory studies of hibernation (Harlow and Menkins 1986, Harlow 1995, Harlow and Frank 2001). Northernmost, peripheral populations are among the most likely populations to experience harsh winter conditions that may necessitate extended, repetitive bouts of deep torpor that constitute hibernation.

The purpose of my study was to document the winter thermoregulation characteristics of black-tailed prairie dogs at the northernmost periphery of the species geographic range, primarily to establish unequivocally whether the species uses hibernation as an over-winter strategy in the wild. To characterize winter thermoregulation and facilitate comparison with previous studies (Harlow and Menkins

1986, Bakko et al. 1988, Harlow 1997, Harlow and Frank 2001, Lehmer et al. 2001, Lehmer et al. 2003), I addressed the following questions regarding thermoregulation of the northernmost prairie dogs in the field: (i) Do seasonal patterns of T_b indicate consecutive, extended torpor bouts that are characteristic of hibernation? (ii) How often do individuals use torpor? (iii) What proportion of the year is spent in a torpid state? (iv) How deep is torpor according to minimum T_b and is there a seasonal trend in depth of torpor? (v) What is the duration of torpor episodes and is there a seasonal trend in duration of torpor? (vi) What are the timing and periodicity of torpor episodes? (vii) Do torpor patterns appear to vary among prairie dogs of different sexes, years, or colonies? (viii) Is use of torpor related to environmental factors such as air temperature and snow conditions? (ix) How synchronous is torpor between prairie dogs, and is the relative synchrony of torpor among individuals that live in close proximity to one another indicative of social thermoregulation?

Methods

I studied black-tailed prairie dogs in the vicinity of the Frenchman River valley in the West Block of Grasslands National Park (49° 07' N 107° 25' W) in southwestern Saskatchewan, Canada, which represents the extreme northernmost periphery of the species geographic range (Hall 1981, Chapter 1). This population of prairie dogs is relatively isolated from southern conspecifics: there are only two known prairie dog colonies within 50 km to the south, the closest of which is located *ca.* 20 km southeast of the study population (Gummer 1999). The northernmost population of prairie dogs inhabits a region that likely subjects prairie dogs to more snow and extreme cold temperatures than any locality of other populations in the genus. During my study, there

were 218 and 219 days with freezing ($T_a \leq 0$ °C) air temperatures during 1999 and 2000, respectively, at the nearest Environment Canada meteorological station (Val Marie, Saskatchewan). Similarly there were 71 and 90 days with snow cover during 1999 and 2000, respectively. The extreme minimum air temperature was -36.5 °C, maximum snow depth was 12 cm, and maximum period of continuous snow cover was 58 d (Environment Canada National Climate Archive 2004).

I live-trapped prairie dogs at two colonies during autumn (October and November) and spring (April and May) by setting wire mesh traps (50 x 15 x 15 cm, custom-built traps and model 202, Tomahawk Live Trap, Tomahawk, Wisconsin) baited with peanut butter and rolled oats. Traps were set near burrow entrances and anchored to the ground with steel stakes. I recorded the geographic coordinates (± 10 m Universal Transverse Mercator zone 13U, North American Datum 1983) of trap locations using a handheld global positioning system (Garmin 12XL, Olathe, Kansas). Each prairie dog was marked with a subcutaneous microchip (12 mm Fecava, Avid Canada, Calgary, Alberta) for reliable identification (Schooley et al. 1993). The microchip was injected dorsally using a sterile 12 gauge hypodermic needle. I determined the sex of each prairie dog and measured body mass (± 10 g) using a spring-scale (Pesola, Switzerland). I could not estimate the age class (e.g., juvenile, yearling, adult; Hoogland 1995) of prairie dogs because the autumn capture period was not conducive to discerning juveniles from yearlings, or yearlings from adults, on the basis of body size, mass, or pelage. To facilitate surgical implantation of dataloggers, prairie dogs were transported a short distance (*ca.* 1 km) on foot to a mobile field surgery (van). I surgically implanted a temperature datalogger (StowAway TidbiT, Onset Computer, Bourne, Massachusetts), coated with physiologically-compatible wax (paraffin/elvax, Mini-mitter, Sun River,

Oregon), in the peritoneal cavity (Lehmer et al. 2001, Lehmer et al. 2003) while the prairie dog was anesthetized by Telazol ($10 \text{ mg} \cdot \text{kg}^{-1}$, tiletamine and zolazepam, Fort Dodge Laboratories, Fort Dodge, Iowa; Woodbury 1996) injection or IsoFlo (isoflurane, Abbott Laboratories, Saint-Laurent, Quebec) administered from a precision vaporizer. Details of the surgical protocol are reported elsewhere (Chapter 5). The wax-coated dataloggers measured 3.5 cm in diameter and 1.9 cm in depth, with a volume of 13 cm^3 and mass of 16 g (*ca.* 2 % of the mean body mass of prairie dogs). The dataloggers measure temperature with an accuracy of $\pm 0.4 \text{ }^\circ\text{C}$ from -5 to $44 \text{ }^\circ\text{C}$ and the accuracy of the real-time clock is ± 1 min per week. I programmed dataloggers to record T_b once every 30 min. After implantation of the datalogger and recovery from anesthesia, prairie dogs were held for 2 to 4 h to monitor their recovery and then I transported them back to the field site to be released at the exact locations from which they had been caught earlier that day. The implanted prairie dogs did not appear to have difficulty with locomotion or navigation: they all promptly maneuvered to burrows. I trapped the same sites during the subsequent spring (April and May) to attempt to recapture any implanted prairie dogs that had not dispersed or died during the intervening winter. For any implanted prairie dogs that I successfully recaptured, I surgically removed the previous datalogger and replaced it with a new datalogger.

To analyze and interpret T_b profiles of implanted prairie dogs, I adopted an operational definition of torpor where torpor was defined by $T_b < 33 \text{ }^\circ\text{C}$ for at least 2 h. In previous field studies of black-tailed prairie dogs, Bakko et al. (1988) documented a mean seasonal minimum T_b of $33.5 \text{ }^\circ\text{C}$, which they interpreted to represent euthermia. Hence Lehmer et al. (2001) used the threshold temperature T_b of $33 \text{ }^\circ\text{C}$ to indicate torpor. By including a 2 h minimum duration in my operational definition of torpor, I

excluded many episodes that would otherwise have appeared as brief, shallow torpor, some of which may have been spurious and caused by the relative accuracy of the datalogger measurements. My approach was conservative and likely resulted in underestimation of the frequency of short-term, shallow deviations from euthermia, which were of secondary interest given that my primary goal was to determine if the species uses hibernation under natural winter conditions. To categorize torpor as hibernation or daily torpor, I considered any torpor bout that extended > 24 h to represent hibernation and any torpor bout < 24 h to represent daily torpor. This classification follows the convention of Geiser and Ruf (1995), who demonstrated justification for categorizing a species use of torpor as either seasonal hibernation or daily torpor, primarily on the basis of the maximum duration of torpor.

For comparison with prairie dog thermoregulation patterns, I obtained daily weather data, describing air temperature and snow depth, from the Environment Canada National Climate Archive (2004) for the meteorological station at Val Marie ($49^{\circ} 22' N$ $107^{\circ} 51' W$), Saskatchewan, which is located approximately 41 km northwest of the centre of my study area. I also measured soil temperature at 2 m depth below the ground surface in a prairie dog colony *ca.* 1 km from my trapping sites, by installing an automatic datalogger (Campbell Scientific CR10X, Edmonton, Alberta) equipped with PVC insulated copper-constantan (type T; ± 1 °C) thermocouple. Black-tailed prairie dogs have been found to occupy burrows at 2 to 3 m depths below the ground surface in more southern localities (e.g., South Dakota; Hoogland 1995).

I quantified deviations from euthermia and estimated frequency of torpor by determining the number of hibernation and daily torpor episodes of each individual prairie dog. I also estimated the cumulative amount of time that was spent in a torpid

state, as well as the relative proportion of that time that was accounted for by hibernation and daily torpor bouts. I quantified depth of torpor by determining the minimum recorded T_b for each torpor episode. I estimated duration of torpor by determining the number of hours between entry and arousal, where entry was defined as the time of day of the last measurement of $T_b \geq 33$ °C prior to torpor and arousal was defined as the time of day of the first $T_b \geq 33$ °C after torpor. To explore whether there were seasonal trends in depth and duration of torpor during hibernation, I estimated linear and curvi-linear (quadratic) regression models with first-order autoregressive errors for each individual prairie dog. I used Akaike's Information Criterion (AIC; Burnham and Anderson 2002) scores to determine whether linear or curvi-linear functions represented better models of seasonal trends in depth or duration of torpor.

To describe the timing of hibernation, I calculated the mean time of day of entries and arousals from hibernation using statistical methods appropriate for circular data distributions (Zar 1999). I applied Rayleigh tests to evaluate the potential significance of the mean time of day for entries and arousals, or alternatively whether the timing of entries and arousals represented uniform circular distributions (Zar 1999). I estimated periodicity by calculating the median amount of time between consecutive entries or arousals of hibernation bouts. To describe the maximum rate of entry and arousal from hibernation, I determined the maximum rate of change between successive T_b measurements for every entry and arousal, and I reported the range of maximum values that were observed.

I examined whether there were significant differences in the mean depth or duration of torpor among prairie dogs of different sexes, years, or colonies, by conducting three-way Analyses of Variance (*ANOVA*) of fixed effects, where the means

were weighted by the number of hibernation bouts that were recorded for each individual. There was no reason to expect biologically significant two- or three-way interactions between the independent variables; therefore, to conserve statistical power (Sokal and Rolff 1995), I did not include interaction terms in the *ANOVA* models.

To explore the potential relationships between the overall proportion of prairie dogs that were torpid and daily air temperature and snow conditions, I calculated the proportion of prairie dogs that were torpid on each day. I applied an arcsine transformation (Krebs 1989) on the proportion of prairie dogs that were torpid and I evaluated linear regression models with first-order autoregressive errors. In addition, as a more robust method of investigating the relationship between torpor and weather conditions, I used a generalized estimating equation approach (Prentice 1988, Zeger et al. 1988) to conduct binary logistic, cross-sectional time series analyses with first-order autoregressive errors. These time series models allowed me to determine if the probability of torpor use by an individual prairie dog was related to daily minimum air temperature or snow depth. I expected that both daily minimum temperature and snow depth were likely to contribute to torpor use. However, given that daily minimum temperature and snow depth were negatively correlated, I estimated separate models for each variable to avoid the potentially confounding effects of multi-collinearity (Zar 1999).

To quantify the synchrony of thermoregulation among prairie dogs, I calculated Pearson correlation coefficients for every combination of two prairie dogs that were monitored simultaneously. I applied a z-transformation (Sokal and Rohlf 1995) and compared the mean z-transformed correlation coefficients (Ruf and Arnold 2000) of any prairie dogs that had been caught at the same or nearby (< 30 m) burrows versus those

that were caught > 30 m apart. I evaluated the significance of the difference between the mean z-transformed correlation coefficients by conducting a randomization test to compare the mean difference with those obtained from 2500 random allocations of the observed correlation coefficients (Manly 1991).

Results

I implanted and released 20 prairie dogs during autumn (12 in November 1999 and 8 in October/November 2000) and I recaptured and recovered dataloggers from 13 prairie dogs during the subsequent spring (7 in April/May 2000 and 6 in April 2001). One adult male prairie dog was represented in both winters. The datalogger that was recovered from one female prairie dog had failed during February 2000, but T_b data recorded prior to its failure had been preserved in nonvolatile memory. The data did not appear anomalous or corrupt and were therefore included in subsequent analyses. Another datalogger that was recovered from a female prairie dog during April 2001 also failed but contained no recoverable data. Thus overall, I monitored thermoregulation of 11 individual prairie dogs for 93 to 365 d · yr⁻¹. The thermoregulation profiles (Figs. 2.1 and 2.2) of the implanted prairie dogs illustrate that they all used extensive, repetitive cycles of hibernation during winter, as well as more shallow daily torpor during autumn, winter, and spring.

Prairie dogs used 8 to 16 hibernation bouts during winter (Table 2.1) and an additional 11 to 35 daily torpor bouts per year (Table 2.2). Cumulatively, they spent 51 to 95 d · yr⁻¹ in a torpid state, 85 to 96 % of which was accounted for by hibernation (Table 2.3). During hibernation, torpor depth ranged from minimum T_b of 7.1 to 11.6 °C (Table 2.1). Every prairie dog exhibited a slightly negative, seasonal trend in minimum

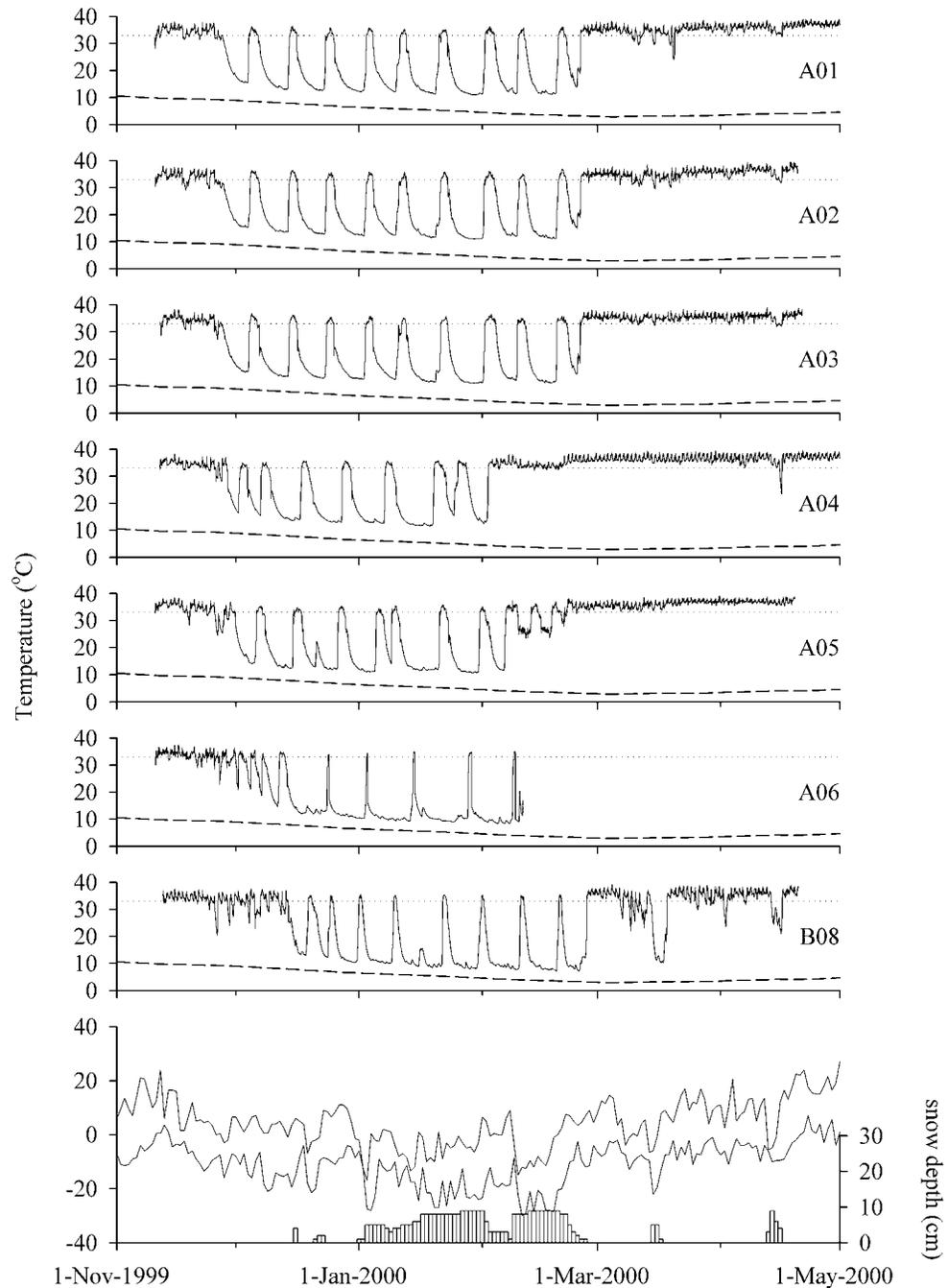


Figure 2.1 Thermoregulation profiles of seven free-living black-tailed prairie dogs during winter 1999/2000. Labels A01 – B08 are identifiers that can be cross-referenced with Figs. 2.3 and 2.5 and Tables 2.1 – 2.5. Periods with $T_b < 33$ °C (dotted line) for at least 2 h were considered to represent torpor. Daily mean soil temperature at 2 m depth is indicated by the dashed lines. The bottom graph indicates daily maximum and minimum air temperatures and the bars indicate daily snow depth (on the secondary ordinate), obtained from the Environment Canada National Climate Data Archive (2004).

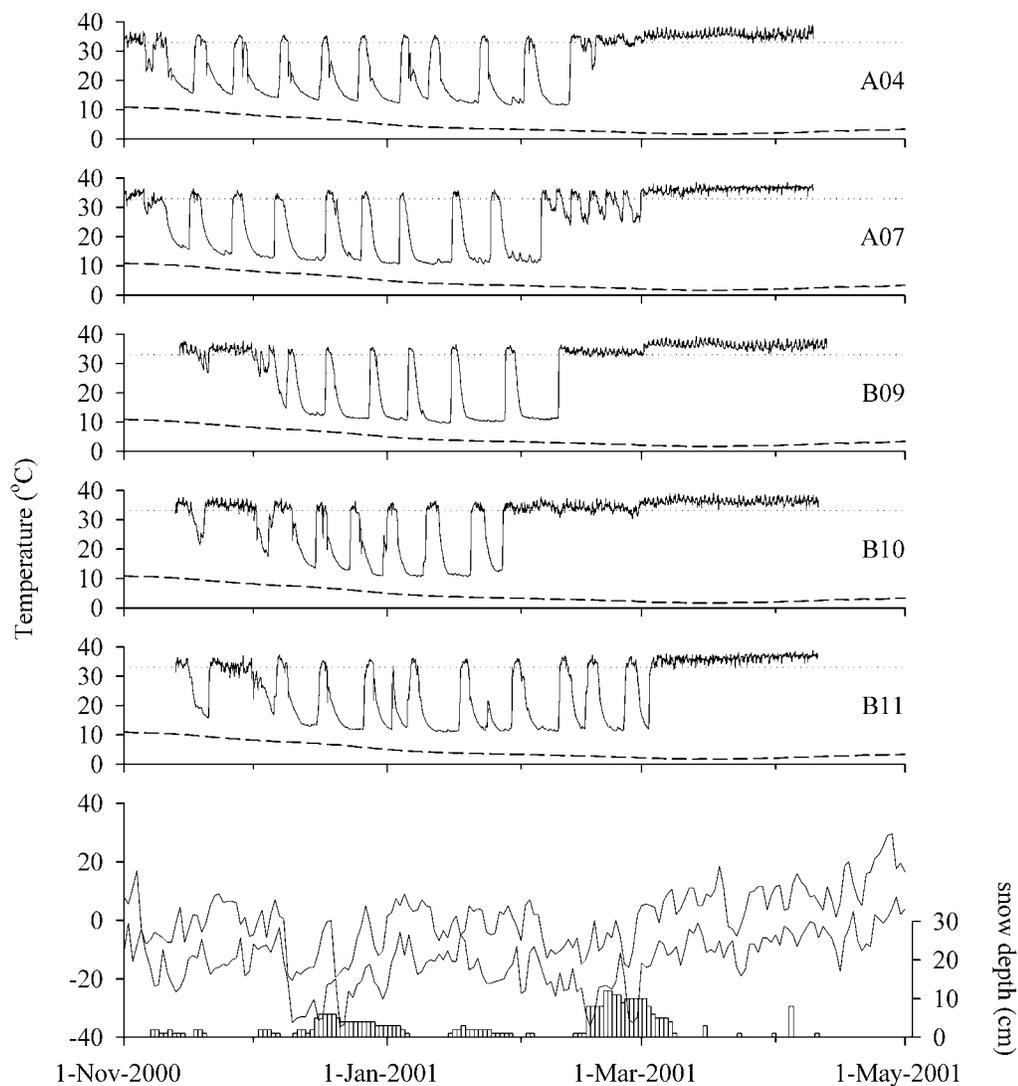


Figure 2.2 Thermoregulation profiles of five free-living black-tailed prairie dogs during winter 2000/2001. Labels A04 – B11 are identifiers that can be cross-referenced with Figs. 2.4 and 2.6 and Tables 2.1 – 2.5. Periods with $T_b < 33$ °C (dotted line) for at least 2 h were considered to represent torpor. Daily mean soil temperature at 2 m depth is indicated by the dashed lines. The bottom graph indicates daily maximum and minimum air temperatures and the bars indicate daily snow depth (on the secondary ordinate), obtained from the Environment Canada National Climate Data Archive (2004).

Table 2.1 Details of hibernation in 11 free-living black-tailed prairie dogs that were implanted with temperature dataloggers at the northernmost periphery of the species geographic range.

| Colony | Years | Individual | Sex | Number of bouts | Minimum T_b (°C) | Maximum duration (d) | Cumulative duration (d) | Earliest date | Latest date |
|----------|---------------------|------------|--------|-----------------|--------------------|----------------------|-------------------------|---------------------|--------------------|
| <i>A</i> | | | | | | | | | |
| | <i>1999 to 2000</i> | | | | | | | | |
| | | A01 | male | 10 | 10.9 | 9.6 | 74.2 | 27 Nov | 25 Feb |
| | | A02 | male | 11 | 10.9 | 9.3 | 77.9 | 17 Nov | 25 Feb |
| | | A03 | male | 11 | 10.9 | 9.4 | 74.6 | 25 Nov | 25 Feb |
| | | A04 | male | 8 | 11.5 | 10.5 | 53.0 | 28 Nov | 2 Feb |
| | | A05 | female | 11 | 10.6 | 10.7 | 67.0 | 25 Nov | 18 Feb |
| | | A06 | female | 9 ¹ | 8.3 | 13.6 | 65.9 ¹ | 28 Nov | 9 Feb ¹ |
| | <i>2000 to 2001</i> | | | | | | | | |
| | | A04 | male | 14 ² | 11.6 | 9.9 | 85.4 | 27 Oct ² | 27 Feb |
| | | A07 | female | 16 | 10.6 | 11.3 | 89.5 | 5 Nov | 28 Feb |
| <i>B</i> | | | | | | | | | |
| | <i>1999 to 2000</i> | | | | | | | | |
| | | B08 | female | 13 | 7.1 | 11.7 | 79.7 | 5 Dec | 16 Apr |
| | <i>2000 to 2001</i> | | | | | | | | |
| | | B09 | male | 8 | 9.7 | 11.1 | 59.1 | 2 Dec | 9 Feb |
| | | B10 | male | 8 | 10.8 | 7.6 | 44.8 | 16 Nov | 27 Jan |
| | | B11 | female | 12 | 11.1 | 10.2 | 80.2 | 15 Nov | 3 Mar |

¹The implanted datalogger failed during February and therefore numbers in this row do not represent the full winter.

²This is the only prairie dog that was monitored continuously throughout the entire year.

Table 2.2 Details of daily torpor in 11 free-living black-tailed prairie dogs that were implanted with temperature dataloggers at the northernmost periphery of the species geographic range.

| Colony | Years | Individual | Sex | Number of bouts | Minimum T_b (°C) | Maximum duration (d) | Cumulative duration (d) | Earliest date | Latest date |
|----------|---------------------|------------|--------|-----------------|--------------------|----------------------|-------------------------|---------------------|--------------------|
| <i>A</i> | | | | | | | | | |
| | <i>1999 to 2000</i> | | | | | | | | |
| | | A01 | male | 17 | 24.0 | 0.8 | 7.8 | 17 Nov | 16 Apr |
| | | A02 | male | 20 | 29.6 | 0.9 | 7.3 | 17 Nov | 16 Apr |
| | | A03 | male | 14 | 30.6 | 0.6 | 3.4 | 17 Nov | 16 Apr |
| | | A04 | male | 15 | 23.3 | 0.8 | 4.4 | 17 Nov | 16 Apr |
| | | A05 | female | 11 | 27.8 | 0.9 | 4.0 | 18 Nov | 24 Feb |
| | | A06 | female | 20 ¹ | 20.7 | 0.8 | 6.0 ¹ | 13 Nov | 5 Dec ¹ |
| | <i>2000 to 2001</i> | | | | | | | | |
| | | A04 | male | 36 ² | 21.2 | 0.7 | 8.9 ² | 31 Aug ² | 4 Apr |
| | | A07 | female | 16 | 29.9 | 0.8 | 5.6 | 20 Oct | 22 Feb |
| <i>B</i> | | | | | | | | | |
| | <i>1999 to 2000</i> | | | | | | | | |
| | | B08 | female | 32 | 20.4 | 1.0 | 13.9 | 18 Nov | 7 Apr |
| | <i>2000 to 2001</i> | | | | | | | | |
| | | B09 | male | 25 | 25.5 | 1.0 | 6.9 | 17 Nov | 1 Mar |
| | | B10 | male | 35 | 23.6 | 0.5 | 6.6 | 16 Nov | 28 Feb |
| | | B11 | female | 18 | 29.3 | 0.8 | 3.9 | 24 Nov | 27 Feb |

¹The implanted datalogger failed during February and therefore numbers in this row do not represent the full winter.

²This is the only prairie dog that was monitored continuously throughout the entire year.

Table 2.3 Cumulative duration of hibernation and daily torpor among 11 free-living black-tailed prairie dogs that were implanted with temperature dataloggers at the northernmost periphery of the species geographic range.

| Colony | Years | Individual | Sex | Cumulative duration (d) | Hibernation component (%) | Daily torpor component (%) |
|----------|---------------------|------------|--------|-------------------------|---------------------------|----------------------------|
| <i>A</i> | | | | | | |
| | <i>1999 to 2000</i> | | | | | |
| | | A01 | male | 82.0 | 91 | 9 |
| | | A02 | male | 85.2 | 91 | 9 |
| | | A03 | male | 78.0 | 96 | 4 |
| | | A04 | male | 57.4 | 92 | 8 |
| | | A05 | female | 71.0 | 94 | 6 |
| | | A06 | female | 71.9 ¹ | 92 ¹ | 8 ¹ |
| | <i>2000 to 2001</i> | | | | | |
| | | A04 | male | 94.2 ² | 91 ² | 9 ² |
| | | A07 | female | 95.1 | 94 | 6 |
| <i>B</i> | | | | | | |
| | <i>1999 to 2000</i> | | | | | |
| | | B08 | female | 93.6 | 85 | 15 |
| | <i>2000 to 2001</i> | | | | | |
| | | B09 | male | 66.1 | 90 | 10 |
| | | B10 | male | 51.4 | 87 | 13 |
| | | B11 | female | 84.1 | 95 | 5 |

¹The implanted datalogger failed during February and therefore numbers in this row do not represent the full winter.

²This is the only prairie dog that was monitored continuously throughout the entire year.

T_b on subsequent hibernation bouts, although the final few torpor bouts of the year were often more shallow, making the overall relationship approximate a quadratic function in all cases (Figs. 2.3 and 2.4, Table 2.4).

Maximum duration of torpor during hibernation ranged from 7.6 to 13.6 d. The majority of prairie dogs exhibited a slightly positive, seasonal trend in duration of torpor, although the final few torpor bouts of the year were often shorter, making the relationship approximate a quadratic function (Figs. 2.5 and 2.6, Table 2.5). One prairie dog (A06), whose datalogger failed during winter, exhibited a linear increase in torpor duration on its first 9 bouts (Fig. 2.5 and Table 2.5) and one prairie dog (B11) exhibited no significant seasonal trend in duration of torpor (Fig. 2.6 and Table 2.5).

Entry into hibernation occurred at all times of day. The mean time of entry was 0:04 h (CST) but the distribution of time of entry did not differ significantly from a uniform circular distribution ($z = 0.083$, $n = 131$, $P = 0.92$). Similarly, arousal from hibernation bouts also occurred at all times of day. The mean arousal time was 11:56 but the distribution of time of arousal did not differ significantly from a uniform circular distribution ($z = 0.167$, $n = 131$, $P = 0.85$). The median periodicity of entries and arousals, respectively, were 9.2 and 9.6 d. Median duration of euthermy between consecutive hibernation bouts was 1.7 d (range 0.1 to 26.1 d). Maximum rate of entry into hibernation varied from 6.8 to 24.5 °C · h⁻¹ and the maximum rate of arousal ranged from 7.6 to 15.0 °C · h⁻¹.

Depth of torpor bouts during hibernation did not differ significantly among male and female prairie dogs ($F_{[1,8]} = 0.350$, $P = 0.57$), but did differ among colonies ($F_{[1,8]} = 11.615$, $P = 0.009$) and years ($F_{[1,8]} = 7.780$, $P = 0.024$). Duration of torpor episodes

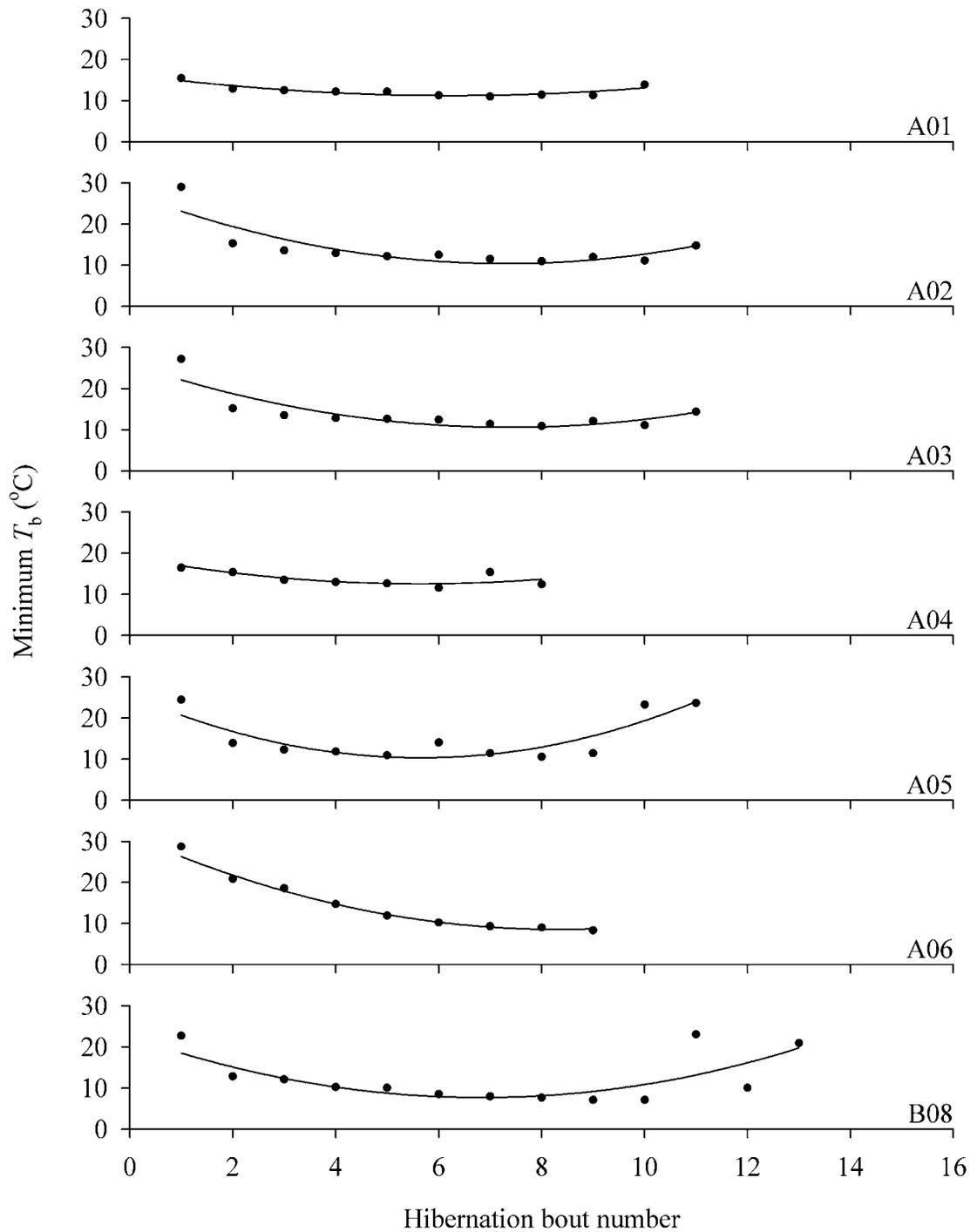


Figure 2.3 Seasonal trends in depth of torpor (minimum T_b) during hibernation among seven free-living black-tailed prairie dogs during winter 1999/2000. Labels A01 – B08 are identifiers that can be cross-referenced with Figs. 2.1 and 2.5 and Tables 2.1 – 2.5. The coefficients and statistical tests for each regression analysis are indicated in Table 2.4.

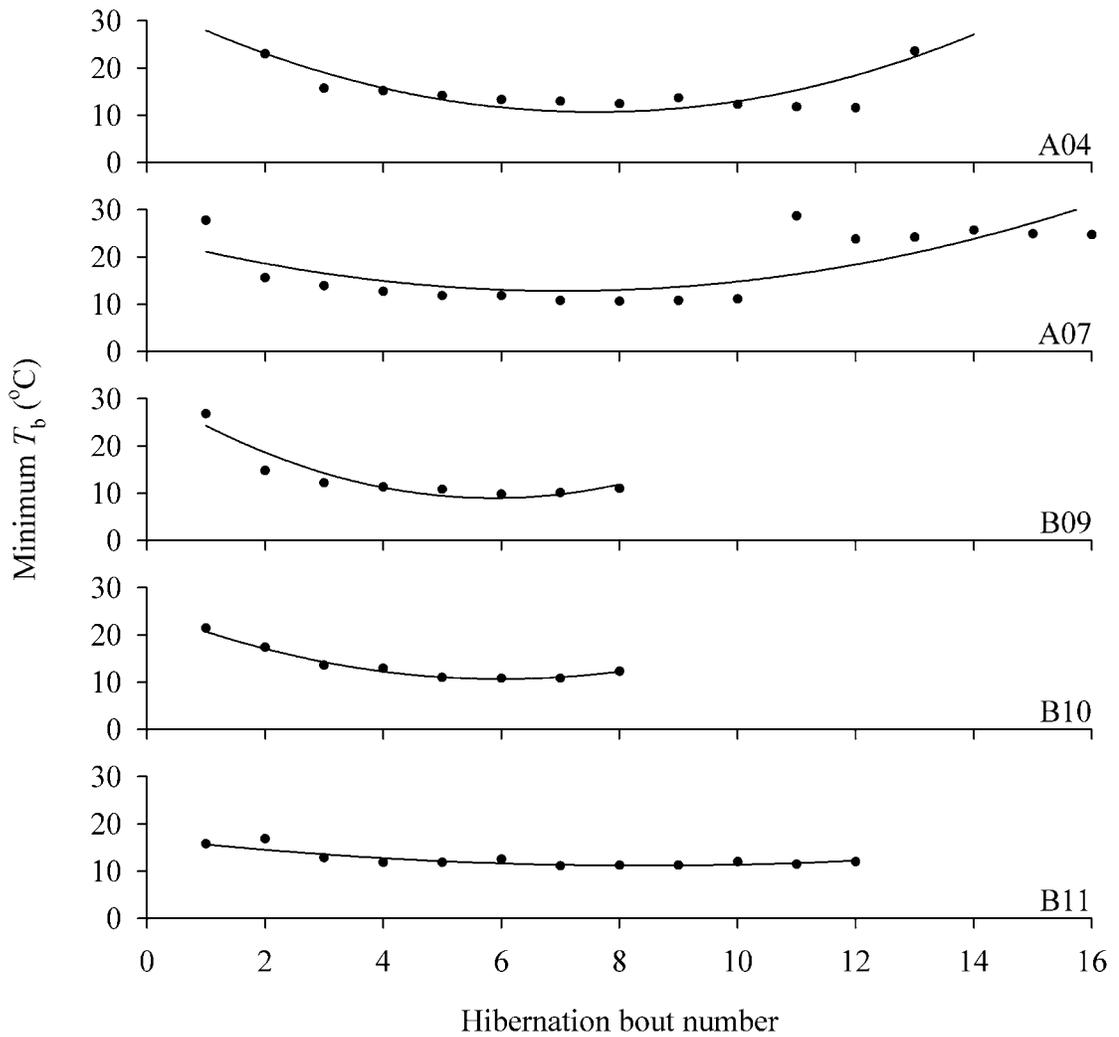


Figure 2.4 Seasonal trends in depth of torpor (minimum T_b) during hibernation among five free-living black-tailed prairie dogs during winter 2000/2001. Labels A04 – B11 are identifiers that can be cross-referenced with Figs. 2.2 and 2.6 and Tables 2.1 – 2.5. The coefficients and statistical tests for each regression analysis are indicated in Table 2.4.

Table 2.4 Regression results for fitting a first-order autoregressive quadratic function to describe the seasonal trend of depth of torpor during hibernation among 11 free-living black-tailed prairie dogs that were implanted with temperature dataloggers at the northernmost periphery of the species geographic range (Figs. 2.3 and 2.4). The independent variable, hibernation bout number, is represented by x .

| Colony | Years | Individual | Sex | x | | | | x^2 | | | |
|----------|--------------|------------|--------|---------|---------|------|--------|---------|--------|------|--------|
| | | | | β | t | df | P | β | t | df | P |
| <i>A</i> | | | | | | | | | | | |
| | 1999 to 2000 | | | | | | | | | | |
| | | A01 | male | -1.567 | -5.407 | 5 | 0.003 | 0.122 | 4.736 | 5 | 0.005 |
| | | A02 | male | -5.003 | -4.136 | 6 | 0.006 | 0.350 | 3.540 | 6 | 0.012 |
| | | A03 | male | -4.493 | -4.242 | 6 | 0.005 | 0.312 | 3.603 | 6 | 0.011 |
| | | A04 | male | -2.778 | -14.397 | 3 | 0.001 | 0.273 | 12.906 | 3 | 0.001 |
| | | A05 | female | -5.139 | -4.948 | 6 | 0.003 | 0.446 | 5.257 | 6 | 0.002 |
| | | A06 | female | -5.911 | -43.043 | 4 | <0.001 | 0.369 | 27.286 | 4 | <0.001 |
| | 2000 to 2001 | | | | | | | | | | |
| | | A04 | male | -5.567 | -6.927 | 9 | <0.001 | 0.360 | 6.864 | 9 | <0.001 |
| | | A07 | female | -3.154 | -2.057 | 11 | 0.064 | 0.221 | 2.529 | 11 | 0.028 |
| <i>B</i> | | | | | | | | | | | |
| | 1999 to 2000 | | | | | | | | | | |
| | | B08 | female | -4.661 | -7.895 | 8 | <0.001 | 0.341 | 8.256 | 8 | <0.001 |
| | 2000 to 2001 | | | | | | | | | | |
| | | B09 | male | -8.475 | -4.081 | 3 | 0.027 | 0.750 | 3.302 | 3 | 0.046 |
| | | B10 | male | -4.880 | -23.081 | 3 | <0.001 | 0.405 | 17.493 | 3 | <0.001 |
| | | B11 | female | -1.483 | -6.674 | 7 | <0.001 | 0.090 | 5.369 | 7 | 0.001 |

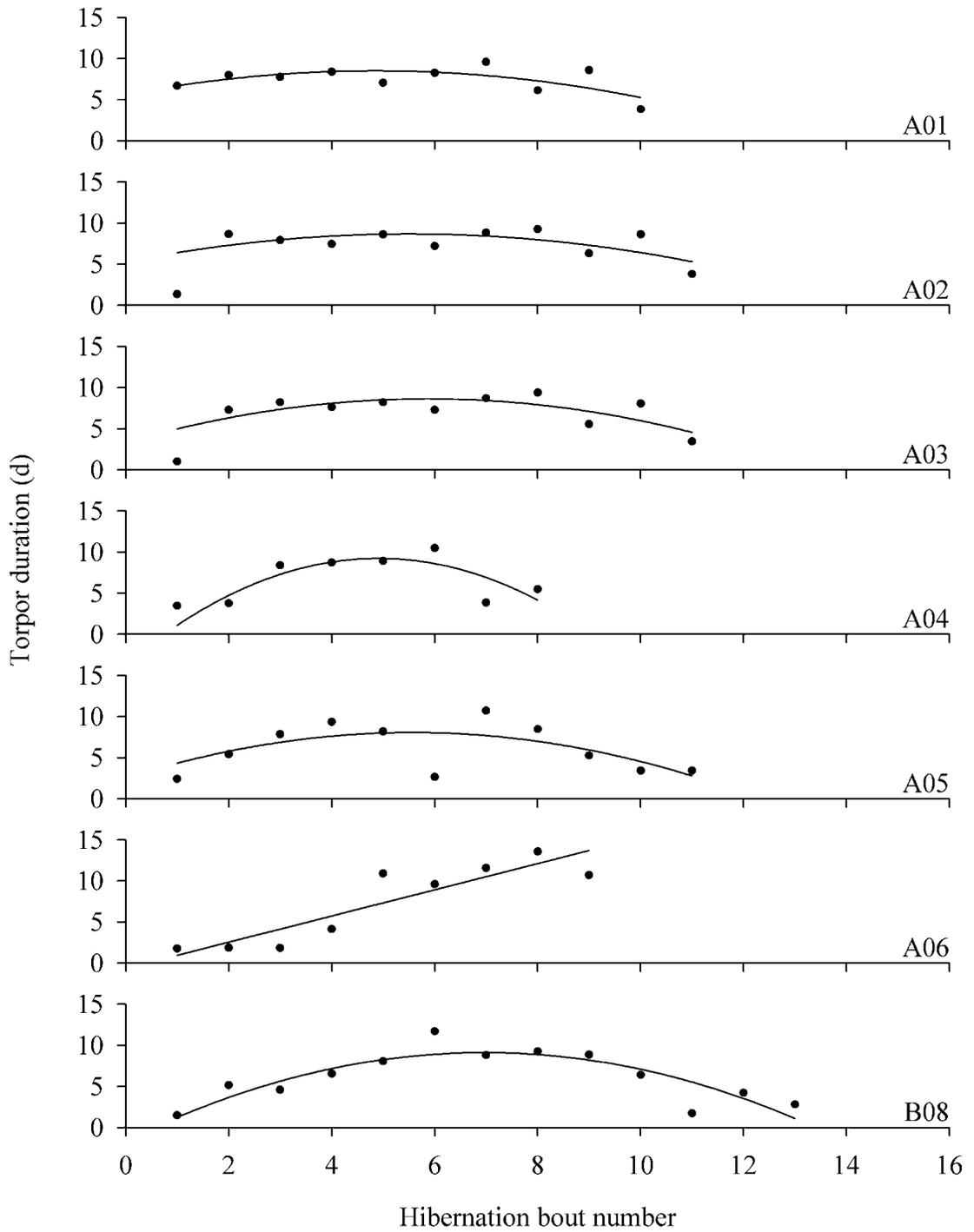


Figure 2.5 Seasonal trends in duration of torpor during hibernation among seven free-living black-tailed prairie dogs during winter 1999/2000. Labels A01 – B08 are identifiers that can be cross-referenced with Figs. 2.1 and 2.5 and Tables 2.1 – 2.5. The coefficients and statistical tests for each regression analysis are indicated in Table 2.5.

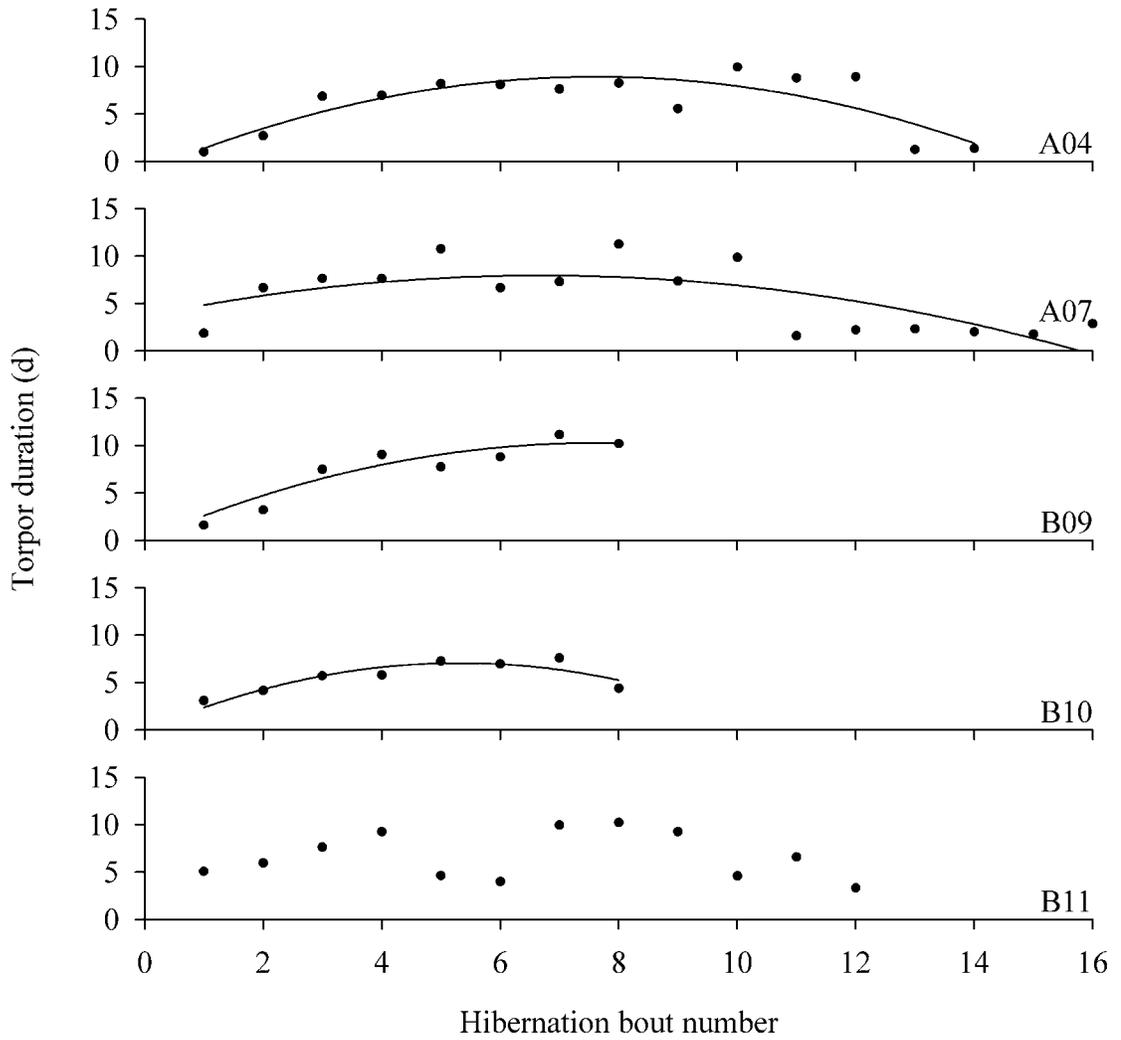


Figure 2.6 Seasonal trends in duration of torpor during hibernation among five free-living black-tailed prairie dogs during winter 2000/2001. Labels A04 – B11 are identifiers that can be cross-referenced with Figs. 2.2 and 2.4 and Tables 2.1 – 2.5. The coefficients and statistical tests for each regression analysis are indicated in Table 2.5.

Table 2.5 Regression results for fitting a first-order autoregressive quadratic function, and in one case a linear function, to describe the seasonal trend of torpor duration during hibernation among 11 free-living black-tailed prairie dogs that were implanted with temperature dataloggers at the northernmost periphery of the species geographic range (Figs. 2.5 and 2.6). The independent variable, hibernation bout number, is represented by x .

| Colony | Years | Individual | Sex | x | | | | x^2 | | | |
|----------|---------------------|------------|--------|---------|--------|------|--------|---------|---------|------|--------|
| | | | | β | t | df | P | β | t | df | P |
| <i>A</i> | | | | | | | | | | | |
| | <i>1999 to 2000</i> | | | | | | | | | | |
| | | A01 | male | 0.886 | 2.449 | 5 | 0.058 | -0.089 | -2.765 | 5 | 0.040 |
| | | A02 | male | 1.360 | 4.245 | 6 | 0.005 | -0.110 | -4.209 | 6 | 0.006 |
| | | A03 | male | 1.926 | 4.843 | 6 | 0.003 | -0.157 | -4.843 | 6 | 0.003 |
| | | A04 | male | 5.441 | 16.073 | 3 | <0.001 | -0.575 | -15.492 | 3 | <0.001 |
| | | A05 | female | 2.097 | 2.853 | 6 | 0.029 | -0.186 | -3.101 | 6 | 0.021 |
| | | A06 | female | 1.680 | 6.088 | 5 | 0.002 | | | | |
| | <i>2000 to 2001</i> | | | | | | | | | | |
| | | A04 | male | 2.552 | 4.547 | 9 | 0.001 | -0.166 | -4.559 | 9 | 0.001 |
| | | A07 | female | 1.253 | 1.841 | 11 | 0.093 | -0.094 | -2.410 | 11 | 0.035 |
| <i>B</i> | | | | | | | | | | | |
| | <i>1999 to 2000</i> | | | | | | | | | | |
| | | B08 | female | 3.369 | 8.794 | 8 | <0.001 | -0.248 | -9.237 | 8 | <0.001 |
| | <i>2000 to 2001</i> | | | | | | | | | | |
| | | B09 | male | 2.926 | 11.144 | 3 | 0.002 | -0.207 | -7.191 | 3 | 0.006 |
| | | B10 | male | 2.268 | 5.549 | 3 | 0.012 | -0.200 | -4.480 | 3 | 0.021 |
| | | B11 | female | 1.389 | 1.656 | 7 | 0.142 | -0.110 | -1.740 | 7 | 0.125 |

during hibernation did not differ significantly among male and female prairie dogs ($F_{[1,8]} = 0.0118, P = 0.878$), nor among colonies ($F_{[1,8]} = 0.014, P = 0.907$) or years ($F_{[1,8]} = 0.054, P = 0.823$).

Comparison of the proportion of prairie dogs that were torpid each day with daily weather data illustrated that all of the implanted prairie dogs used torpor primarily during, but not limited to, periods of cold air temperatures and continuous snow (Figs. 2.7 and 2.8). In 1999, prairie dogs began hibernating in mid- to late-November, *ca.* 1 month prior to the arrival of snow despite relatively mild daytime T_a (maximum daily $T_a > 0^\circ\text{C}$; Fig. 2.7). Prairie dogs in 2000 began hibernation at approximately the same time of year, well after the arrival of snow and cold T_a (Fig 2.8). The proportion of prairie dogs that were torpid did not appear to be significantly related to daily minimum T_a during either of the two winters of study ($t_{[155]} = -1.035, P = 0.302$ and $t_{[145]} = -1.469, P = 0.14$, respectively). The proportion of prairie dogs that were torpid was significantly positively related to snow depth during the first winter ($t_{[155]} = 2.393, P = 0.018$) but not during the second winter ($t_{[145]} = -0.982, P = 0.328$). On an individual basis, the probability of a prairie dog using torpor on a given day was significantly negatively related to daily minimum T_a and positively related to snow depth (Table 2.6).

I determined that three prairie dogs that were caught in close proximity to one another had highly synchronous T_b profiles, particularly during hibernation bouts (Fig. 2.9). The mean (\pm SE) Fisher z-transformed correlation coefficient between the T_b profiles of these individuals was 2.45 ± 0.13 ($n = 3$) whereas the mean correlation coefficient among all the other combinations of prairie dogs that were monitored simultaneously was 0.55 ± 0.15 ($n = 28$). A randomization test indicated that the

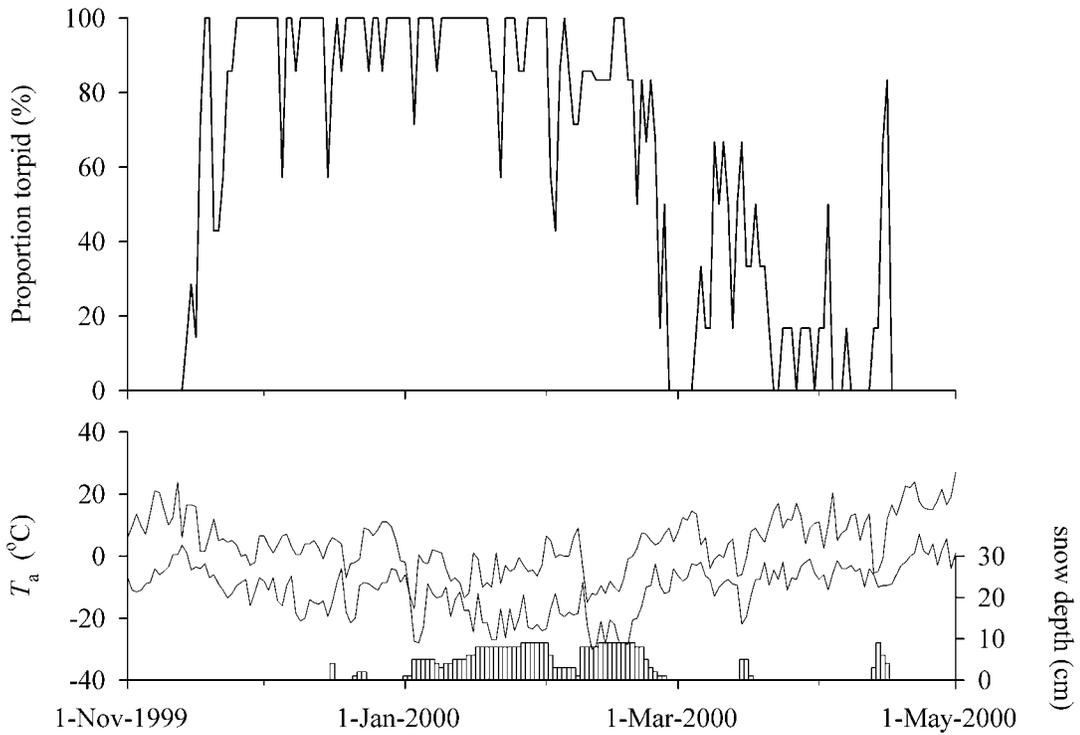


Figure 2.7 The proportion of individuals that used torpor each day among seven free-living black-tailed prairie dogs during winter 1999/2000. The bottom graph indicates daily maximum and minimum air temperatures and the bars indicate daily snow depth (on the secondary ordinate), obtained from the Environment Canada National Climate Data Archive (2004).

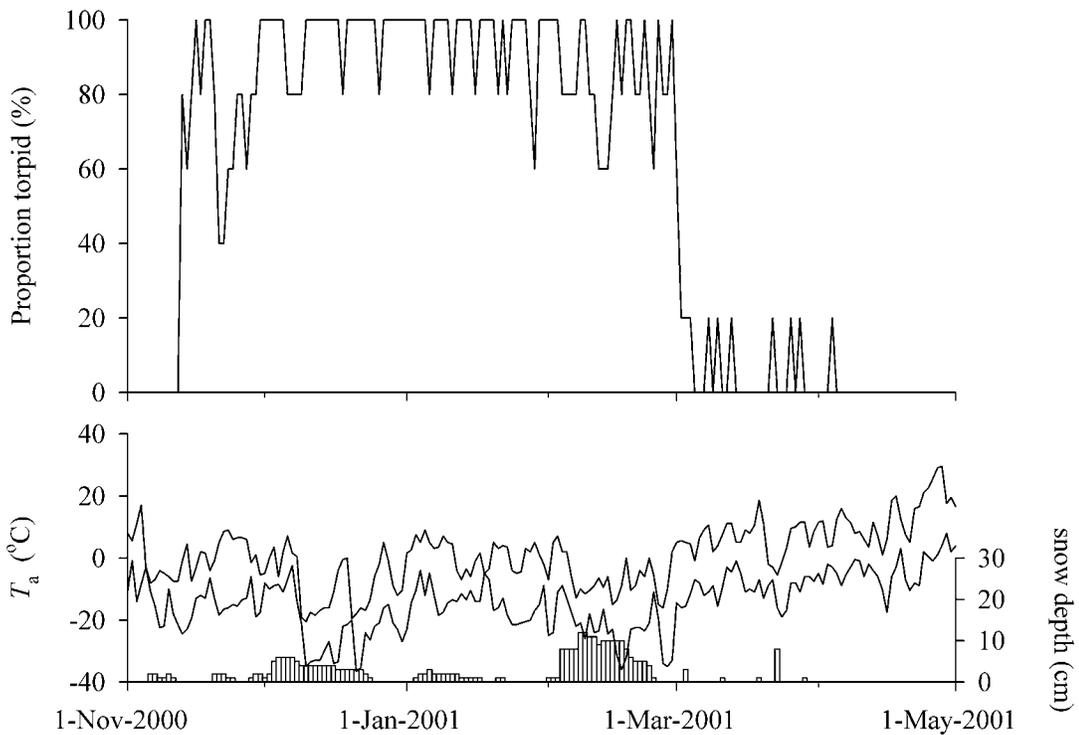


Figure 2.8 The proportion of individuals that used torpor each day among five free-living black-tailed prairie dogs during winter 1999/2000. The bottom graph indicates daily maximum and minimum air temperatures and the bars indicate daily snow depth (on the secondary ordinate), obtained from the Environment Canada National Climate Data Archive (2004).

Table 2.6 Cross-sectional time series analysis results of separate models relating daily minimum air temperature and snow depth to probability of torpor among 11 free-living black-tailed prairie dogs. The total number of observations was 2107 with an average number of observations per individual of 192 (range 93 to 516).

| Independent variable | Mean value (\pm SD) | | Odds ratio (95% CI) | β (95% CI) | z | P |
|---|------------------------|-------------|------------------------|-------------------------|--------|--------|
| | Torpor | Normothermy | | | | |
| Minimum air temperature ($^{\circ}$ C) | -16.3 (8.0) | -5.4 (8.9) | 0.95 (0.94, 0.96) | -0.054 (-0.067, -0.041) | -8.090 | <0.001 |
| Snow depth (cm) | 3.0 (3.4) | 0.8 (2.2) | 1.15 (1.10, 1.21) | 0.143 (0.095, 0.192) | 5.800 | <0.001 |

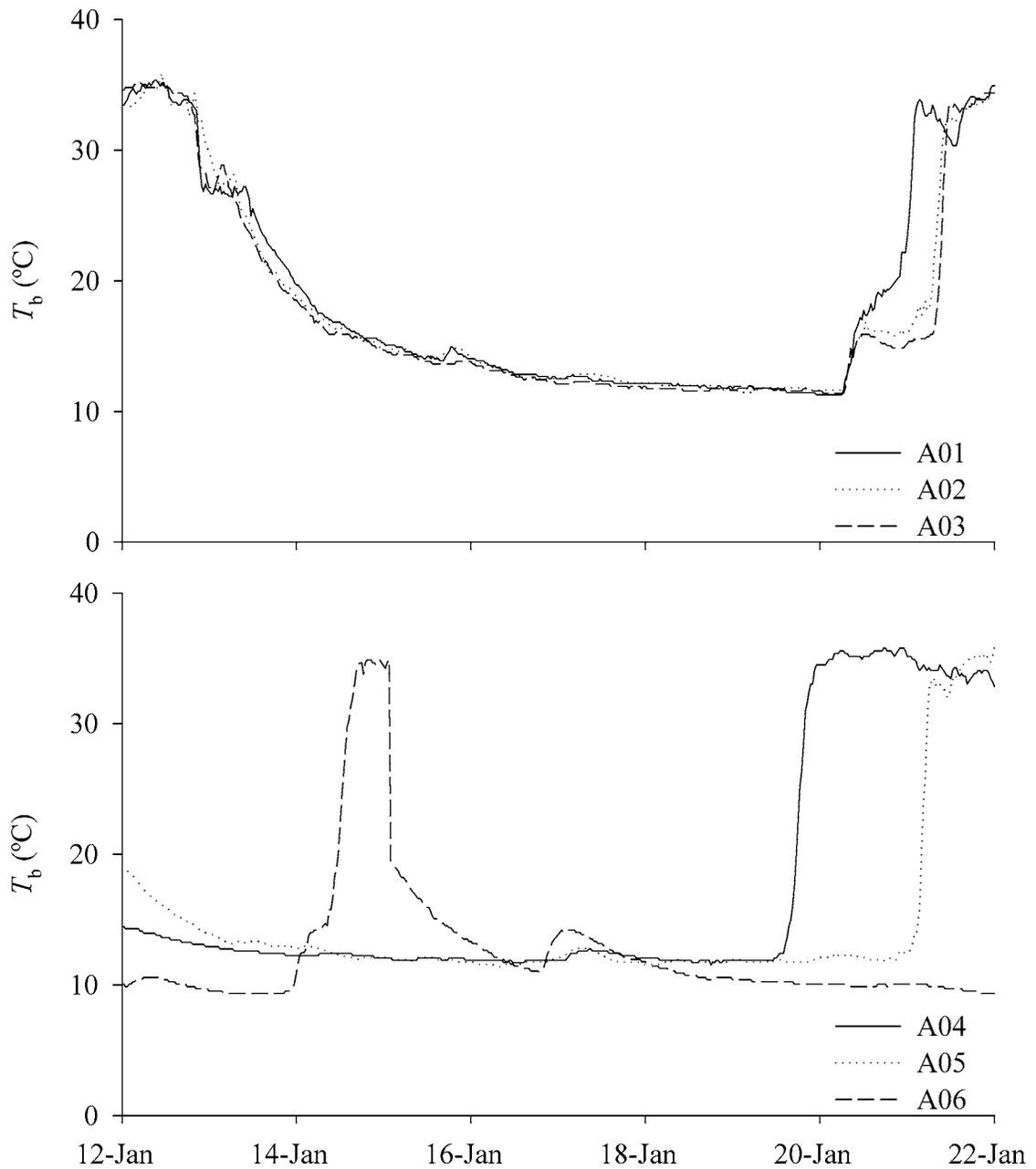


Figure 2.9 Thermoregulation during hibernation over a representative period of 10 days for six free-living black-tailed prairie dogs that were monitored in the same colony during winter 1999/2000. The top graph shows T_b profiles of three prairie dogs that were all caught near the same burrow and exhibited a high degree of synchrony whereas the bottom graph shows T_b profiles of three prairie dogs that were caught > 30 m apart and are not as synchronous.

observed difference between the mean correlation coefficients was highly significant ($P < 0.001$).

Discussion

I have demonstrated that free-living black-tailed prairie dogs at the northernmost periphery of the species geographic range use consecutive, deep bouts of torpor that constitute hibernation. This finding is not consistent with the general belief that the species does not hibernate (Hoogland 1995, Hoogland 1997, Lehmer and Van Horne 2001), nor is it consistent with the thermoregulation patterns that have been documented in southern conspecifics in the wild (Bakko et al. 1988, Lehmer et al. 2001, Lehmer et al. 2003) and in laboratory studies (Harlow and Menkins 1986, Harlow 1997, Harlow and Frank 2001). The torpor patterns of northern prairie dogs are more similar to those of “classical” hibernators such as the Richardson’s ground squirrel (*Spermophilus richardsonii*; Wang 1979, Michener 1992). Unfortunately, there are no published reports of natural thermoregulation profiles of any of the three species of prairie dogs that are presumed to hibernate (Stockard 1929, Tileston and Lechleitner 1966, Bakko and Brown 1967, Bakko 1977, Clark 1977, Hoogland 1995), with which to compare my findings. However, studies of white-tailed prairie dogs in captivity have indicated hibernation bouts of comparable depth, duration, and frequency (Bakko and Nahorniak 1986, Harlow and Menkins 1986, Harlow and Frank 2001) as I documented for northern prairie dogs. The prairie dogs of my study did not use torpor exclusively during periods of winter freezing ($T_a < 0$ °C) temperatures and snow. Hence it appears that northern black-tailed prairie dogs in the wild have similar hibernation patterns as “representative spontaneous hibernators” (Harlow and Menkins 1986, Harlow 1995, Harlow 1997).

Although this finding is contradictory to previous studies of southern conspecifics (Harlow and Menkins 1986, Bakko et al. 1988, Lehmer et al. 2001, Lehmer and Van Horne 2001, Lehmer et al. 2003), more importantly it makes black-tailed prairie dogs a clear example of a species that displays substantial intraspecific, geographic variation in thermoregulation and energetics across its range.

Northern black-tailed prairie dogs exhibited substantial deviations from euthermy, with the magnitude of all measures of torpor being unprecedented for this species in the literature. Depth of torpor, duration, frequency, and cumulative proportion of time in torpor all were consistently much greater than had been described by comparable field studies near the centre of the species geographic range (Lehmer et al. 2001, Lehmer et al. 2003). Most notably, northern prairie dogs spent a considerable amount of time (51 to $95 \text{ d} \cdot \text{yr}^{-1}$) in a torpid state, up to an order of magnitude more time than southern conspecifics in Colorado (7.2 and $8.2 \text{ d} \cdot \text{yr}^{-1}$ for males and females, respectively; Lehmer et al. 2003). Similarly, northern prairie dogs used torpor to a much greater extent than had ever been reported from laboratory studies, including experiments in which prairie dogs were deprived of food and water at cold T_a (Harlow and Menkins 1986, Harlow 1997) and exposed to a diet artificially enriched with polyunsaturated fatty acids to enhance torpor (Harlow and Frank 2001). The hibernation patterns of northern black-tailed prairie dogs also appear to be more consistent and predictable (periodic) than those of southern conspecifics, although I was not able to evaluate this because quantitative descriptions of periodicity of torpor patterns have not been reported previously.

The seasonal trends that I documented in depth and duration of torpor during hibernation are similar to those of other hibernators (e.g., Wang 1979, French 1986,

Barnes 1989, Michener 1992). Frequently attention has focused on preliminary “test drops” that are evident from generally increasing depth and duration of early season torpor bouts, implying simple linear or rank order relationships (Strumwasser 1960, Scott et al. 1974, Pivorun 1976, Lyman et al. 1982, Zervanos and Salsbury 2003). However, shallower torpor of shorter duration is common in both early- and late-season hibernation (Wang 1979, French 1986, Barnes 1989, Michener 1992). It seems unexpected that hibernators should use shallow torpor of shorter duration during late winter when soil temperatures are typically near the seasonal minimum (Wang 1979, Michener 1992) and food is presumably scarce. Yet there is potential adaptive value of hibernators spending a greater proportion of time in a euthermic state during late winter hibernation so as not to inadvertently compromise early spring reproduction (French 1986, Kenagy 1986).

In my statistical models of seasonal trends and relationships between environmental conditions and torpor use, I also accounted for potential temporal autocorrelation because such serial correlation itself can appear as a trend (Manly 1991). It is important not to misrepresent consecutive torpor bouts within a time series of observations of an individual as independent observations. My results illustrate that autocorrelation is an important component to be considered when torpor depth, duration, and other measures are likely to occur in a particular order and are consistent within individuals. Treatment of such observations as independent in subsequent statistical tests, or even summary statistics, is problematic due to both simple pseudoreplication and temporal pseudoreplication (*sensu* Hurlbert 1984). The majority of previous torpor studies pooled different numbers of measurements from different individuals and simply analyzed or provided descriptive statistics on variables of interest without providing

information on the relative distribution of the data among different individuals (e.g., Harlow and Frank 2001, Lehmer et al. 2001, Lehmer et al. 2003). Aside from one recent study of hibernating black bears (*Ursus americanus*; Harlow et al. 2004), I found no other example of an autoregressive time series approach to analyses of hibernation or torpor, despite the fact that thermoregulation data are almost always repeatedly measured within individuals over time. I suggest that thermoregulation studies should account for relative dependence of observations by conducting autoregressive analyses or applying repeated measures experimental designs. These approaches should facilitate reporting of meaningful torpor patterns without warranting suspicion about the relative effects of pseudoreplication on statistical outcomes.

I found that the time of day for entry and arousal from hibernation bouts was highly variable among northern black-tailed prairie dogs, with no significant trends towards certain times of day. In contrast, Lehmer et al. (2003) indicated that southern conspecifics tended to enter and arouse from periodic torpor between 11:00 and 16:00; they interpreted the distinct timing of entry and arousal as evidence of an innate timing mechanism. One reason that northern prairie dogs may exhibit much more variable timing of entry and arousal may be related to the much larger proportion of time that is spent in a torpid state: the less time that individuals are euthermic and active in their underground burrows or aboveground, the fewer extrinsic cues that they can presumably receive regarding photoperiod for maintaining precise circadian periodicity.

Hibernation depth and duration of northern prairie dogs do not appear to vary substantially among the sexes. Although there can be substantial sex differences in torpor patterns of some other hibernating sciurids (e.g., *S. richardsonii*; Michener 1992), this does not appear to be the case for more social species that nest communally (e.g.,

Marmota marmota; Ruf and Arnold 2000). Behavioural ecology of black-tailed prairie dogs in more central regions of the species geographic range is well documented; prairie dogs of the same harem-polygynous family groups are known to share burrows (Hoogland 1995). Presumably northern prairie dogs nest communally during winter, which should cause the depth and duration of torpor to be similar because T_b patterns of individuals would presumably affect each other through passive heat loss facilitated by proximity in underground nests. On average, sex differences in torpor depth and duration would therefore not be expected unless there was sex-assortative nesting during winter, which seems unlikely based on the degree of sociality of black-tailed prairie dogs (King 1955, Hoogland 1995). Given the sociality of northern black-tailed prairie dogs and that they are now known to hibernate, the northern population provides a newfound opportunity for studying the interactions between social behaviour and hibernation.

Although there did not appear to be a significant difference in the torpor patterns of the sexes, I did document that depth of torpor varied between different years of study and among colonies. This suggests that depth of torpor is affected by annual and local variations in climate/microclimate, or possibly associated differences in vegetation communities that may impose dietary differences. Soil temperatures (Barnes 1989, Michener 1992, Zervanos and Salsbury 2003) and diet composition (Harlow and Frank 2001, Munro and Thomas 2004) are known to influence depth of torpor of many hibernators. The amount of dietary polyunsaturated fatty acids has been shown to affect the depth and duration of torpor among captive black-tailed and white-tailed prairie dogs (Harlow and Frank 2001). Regardless of the underlying cause of variation in depth of torpor among years and colonies, it is important to account for this variation in statistical

analyses so that it does not confound analysis of other potential variables of interest (e.g., potential sex differences).

The proportion of northern prairie dogs that were torpid on a given date did not appear to be related to minimum daily T_a but was related to daily snow depth in one of two years of study. Unfortunately I was unlikely to find significant relationships between ambient conditions and the proportion of prairie dogs that were torpid because the proportion of individuals that were torpid was highly autocorrelated. Furthermore, the effective sample size that I used for calculation of the daily proportions ($n = 7$ and $n = 5$ prairie dogs in the two years of study, respectively) was relatively small and the nature of prairie dogs' hibernation patterns was such that there was not much variation in the proportion of animals that were torpid on a daily basis (e.g., see Figs. 2.7 and 2.8). Hence this type of analysis would be better applied to studies with large sample sizes and more sizable variation relative to the observed serial correlation.

At the level of the individual prairie dog, I found that probability of torpor use was highly significantly related to both daily minimum T_a and snow depth. Yet northern prairie dogs did not use torpor exclusively during periods of freezing ($T_a < 0$ °C) temperatures and snow cover: they entered hibernation at approximately the same time of year during autumn regardless of whether snow and freezing T_a had arrived, suggesting that they spontaneously entered torpor without requiring inducement from extreme cold and starvation. Hence the hibernation behaviour exhibited by northern black-tailed prairie dogs appears to be more similar to that of white-tailed prairie dogs than of southern conspecifics (Harlow and Menkins 1986, Harlow 1997). However, northern prairie dogs were also clearly more likely to use torpor on days with low T_a and deep snow cover. The generalized estimating equation approach (Prentice 1988, Zeger et

al. 1988) that I used to document this general pattern of torpor use was an effective means of examining the general relationships between environmental conditions and probability of torpor, given simultaneous time series data from multiple individuals.

Three prairie dogs that I caught near the same burrow had highly synchronous T_b profiles. Comparison of correlation coefficients of pairs of prairie dogs that had been caught > 30 m apart indicated that the high degree of synchrony that I observed in the three prairie dogs was highly unlikely to have occurred by random chance. Given that black-tailed prairie dogs are known to have common burrows that are shared with other prairie dogs in the family group (Hoogland 1995), individuals are likely to share winter nests. Communal nesting should increase the likelihood of synchrony among individuals because conduction of heat between prairie dogs in the group should cause T_b to be similar. Furthermore, arousal by one or more individuals would likely instigate arousal by other individuals through passive heat loss, as appears to be the case among alpine marmots (*Marmota marmota*; Ruf and Arnold 2000). Subtle differences in the timing of energetically costly arousals could potentially reduce the energetic burden of arousal for all individuals if it were conducted synchronously, or alternatively it could increase the burden of arousal for the lead individuals if they try to actively arouse before others in the nest. Accordingly, Ruf and Arnold (2000) showed that the degree of group synchrony in hibernation was the most important factor determining over-winter mass loss of alpine marmots. Hence social hibernation provides opportunities for parental care and kin selection. It is possible that some prairie dogs in poor body condition, that would not be able to survive if they were required to nest solitarily, survive the winter by nesting with family members that assist arousal of the group through passive conduction of heat (Arnold 1988, 1990, 1993).

Interactions between social behaviour and hibernation are likely to be valuable areas of future research on northern prairie dogs given that they may be among the most social of all ground-dwelling hibernators. Previous theoretical perspectives (Armitage 1981, Michener 1983, Michener 1984) relating sociality and hibernation have in part been predicated upon presumptions about behaviour and circannual rhythms of prairie dogs, such as the general belief that the most social species of the prairie dogs does not hibernate. It would be useful to revisit these perspectives with new knowledge of geographic variation in hibernation patterns to determine if theoretical perspectives need to be refined or if they point towards new questions or research opportunities that had not arisen previously.

Clearly, the question of whether the capability of hibernation is an endemic, genetically controlled characteristic of northern prairie dogs remains to be addressed. Alternatively, one might ask whether southern conspecifics would also exhibit hibernation if they were acclimatized to comparable conditions. However, the comparatively infrequent, shallow torpor exhibited by southern conspecifics in field studies (Bakko et al. 1988, Lehmer et al. 2001, Lehmer et al. 2003) and laboratory experiments (Harlow and Menkins 1986, Harlow 1997, Harlow and Frank 2001) suggests that the capability of hibernation may be limited to northern prairie dogs. Furthermore, recurrence of expression of ancestral traits that facilitate hibernation (Malan 1996, Geiser 1998, Lovegrove et al. 1999, Grigg and Beard 2000) would presumably be favoured by the relative geographic isolation of northern prairie dogs (Gummer 1999) in a harsh winter climate compared to southern conspecifics. Regardless whether the capability of hibernation among northern black-tailed prairie dogs has a genetic basis or represents phenotypic plasticity, northern prairie dogs provide a

newfound opportunity for studying the expression of torpor through intraspecific and interspecific comparative studies.

Conclusion

Black-tailed prairie dogs have not been considered to use consecutive, deep torpor that constitutes hibernation (Bakko et al. 1988, Hoogland 1995, Hoogland 1997, Lehmer and Van Horne 2001) and this belief has contributed to comparative physiological approaches (Harlow and Menkins 1986, Harlow 1995, Harlow 1997, Harlow and Frank 2001, Lehmer et al. 2001) and theoretical perspectives in behavioural and evolutionary ecology (Armitage 1981, Michener 1983, Michener 1984). However, I observed that the northernmost population of black-tailed prairie dogs, which appears to experience the harshest winter climate of any population in the genus, uses hibernation as an over-winter strategy. Individuals adopt consecutive, deep bouts of torpor with the cumulative amount of time in torpor ranging from 51 to 95 d · yr⁻¹. The hibernation patterns of northern black-tailed prairie dogs are comparable to those that white-tailed prairie dogs exhibit under experimental conditions in captivity (Harlow and Menkins 1986, Harlow 1997, Harlow and Frank 2001). Hence black-tailed prairie dogs are a striking example of a species that displays substantial intraspecific, geographic variation in thermoregulation and energetics across a climatic gradient. As such, prairie dogs likely represent a good candidate study system for comparative intraspecific and interspecific studies of thermoregulation and expression of hibernation. My results also underscore the importance of not inadvertently generalizing findings among populations of a species that may in fact be adapted to a broader range of conditions than has been studied to date.

CHAPTER 3. WINTER TORPOR IN THE NORTHERNMOST ORD'S KANGAROO RATS (*DIPODOMYS ORDII*)

Introduction

Kangaroo rats (*Dipodomys*) are nocturnal granivores that are renowned for their adaptations for survival of difficult conditions (MacMillen 1983, French 1993, Tracy and Walsberg 2002). They possess a host of adaptations that facilitate survival in particularly hot and dry, desert environments (French 1993). Comparatively little is known about their winter behaviour, thermoregulation, and energetics despite the fact that other members of the family Heteromyidae, the kangaroo mice (*Microdipodops*) and pocket mice (*Chaetodipus* and *Perognathus*), are known to use extensive daily torpor and hibernation (Bartholomew and MacMillen 1961, Tucker 1962, Tucker 1965, Tucker 1966, Brown and Bartholomew 1969, Wang and Hudson 1970, Browher and Cade 1971, French 1977, Meehan 1977, Wolff and Bateman 1978, MacMillen 1983, French 1989, French 1993). In a review of the physiological ecology of heteromyid rodents, French (1993) indicated that torpor appears to be poorly developed in the kangaroo rats, given that shallow torpor has only been induced in kangaroo rats through starvation to a near-death state in laboratory studies of four species: Merriam's kangaroo rats (*D. merriami*; Dawson 1955, Carpenter 1966, Yousef and Dill 1971), panamint kangaroo rats (*D. panamintinus*; Dawson 1955), chisel-toothed kangaroo rats (*D. microps*; Breyen et al. 1973), and desert kangaroo rats (*D. deserti*; MacMillen 1983).

In these experiments, most captive kangaroo rats that exhibited torpor subsequently died (Dawson 1955, Carpenter 1966, Yousef and Dill 1971, Breyen et al. 1973, MacMillen 1983). Based on laboratory studies, MacMillen (1983:70) summarized that there was “no convincing evidence that torpor in *Dipodomys* spp. is an ecologically meaningful phenomenon.” However, the limited torpor capabilities observed in kangaroo rats under extreme starvation in captivity may not be adequately representative of the animals under more natural conditions. Furthermore, it is unclear to what extent these laboratory findings may be representative of other species and populations of kangaroo rats in which thermoregulation has not been studied.

Several field studies have described winter activities and energetics of free-living kangaroo rats. Kangaroo rats are observed aboveground and caught throughout the year in the majority of locales (Reynolds 1958, Kenagy 1973, O’Farrell 1974, Nagy and Gruchacz 1994), even when air temperature approaches -19°C (Kenagy 1973, O’Farrell 1974) and when there is partial (up to 40 %) snow cover (Mullen 1971, Kenagy 1973, O’Farrell 1974). However, it may be erroneous to presume that kangaroo rats do not use daily torpor or seasonal hibernation in the wild simply because some individuals are active aboveground throughout the year; kangaroo mice and pocket mice are also active aboveground year-round but are known to use both daily torpor and hibernation (Brown and Bartholomew 1969, O’Farrell et al. 1975, French 1993). Kangaroo rats also store large quantities of seeds in their underground burrows; their reliance on cached seeds appears to be a primary means of survival of periods during which the availability of new food is limited (Herrera et al. 2001). Kenagy (1973) concluded that one chisel-toothed and one Merriam’s kangaroo rat in the rain shadow of the Sierra Nevada in eastern California did not use torpor during winter given that neither individual was

sedentary in its underground burrows for more than 2.7 h at a time. Nagy and Gruchacz (1994) found no evidence of torpor in 22 Merriam's kangaroo rats during winter in the Mohave Desert in California according to estimates of field metabolic rates (*FMR*). However, Mullen (1971) estimated low *FMR* for an unspecified, small number of Merriam's kangaroo rats and one chisel-toothed kangaroo rat in the Mohave Desert in Nevada, and speculated that low *FMR* estimates may have suggested use of daily torpor.

It is remarkable that there continues to be considerable uncertainty regarding thermoregulation and energetics of kangaroo rats, given that the genus has been subject to extensive research on physiological adaptations (French 1993). This uncertainty could be clarified by field studies of thermoregulation in kangaroo rats that inhabit relatively high latitude or altitude environments. Ord's kangaroo rat (*D. ordii*) has the most extensive distribution of any species in the genus (Schmidly et al. 1993). It has been observed aboveground year-round at moderately high latitude and altitude (O'Farrell 1974). However, at the extreme northernmost periphery of the species range in Canada, kangaroo rats remain in their underground burrows for several months during winter (Gummer 1997). Previously, I recorded possible evidence of torpor among free-living, northern Ord's kangaroo rats by conducting radio telemetry monitoring of individuals fitted with external, temperature sensitive radio-collars (Gummer 1997). Radio-collared kangaroo rats appeared to use shallow, daily torpor during early winter, with a minimum recorded skin temperature (T_{sk}) of 17.5 °C and maximum known torpor duration of 8.25 h. The limitations of this work included: (i) I could not quantify the extent to which T_{sk} approximated T_b (Barclay et al. 1996, Willis and Brigham 2003) and therefore it was uncertain whether the circadian T_{sk} variations that I recorded reflected torpor or instead reflected different levels of activity or microclimate variation; (ii) the data were limited

due to irregular, intermittent measurements of T_{sk} and the short battery-life of the radio-collars, and therefore the frequency with which individuals used torpor was unclear; (iii) accordingly, I could not precisely characterize the depth of torpor (minimum T_{sk}) of individuals nor examine whether depth of torpor increased during the course of the winter; (iv) I could not adequately characterize duration of torpor for individuals, nor determine whether torpor duration increased over the course of the winter; and most importantly, (v) I did not recapture individual kangaroo rats that displayed torpor bouts and therefore I could not be confident that they survived the winter. Consequently, I could not exclude the possibility that the apparent torpor bouts were induced by drastic mass loss and culminated in death, which would have been analogous to laboratory observations of torpor during starvation and imminent death in other species of kangaroo rats (Dawson 1955, Carpenter 1966, Yousef and Dill 1971, Breyen et al. 1973, MacMillen 1983). This would support previous assertions by French (1993) and MacMillen (1983) that the ecological significance of torpor in kangaroo rats may be negligible. Given the equivocal results from this earlier study, effective field studies are needed to clarify thermoregulation of kangaroo rats and to provide a better context for ultimately understanding potential variation in torpor capabilities among species and populations within the genus. Furthermore, there has been a strong emphasis on the physiological ecology of these rodents' adaptations for surviving hot and dry conditions (French 1993, Tracy and Walsberg 2002) and there is a concomitant lack of knowledge of their winter ecology, this being particularly relevant to several species of kangaroo rats that are distributed across major climatic gradients. The northernmost population of Ord's kangaroo rats is an appropriate starting point to investigate thermoregulation in

the genus because the population presumably occupies a more difficult winter climate than any other population (Appendix B).

Therefore my main goal was to document the winter thermoregulation characteristics of Ord's kangaroo rats at the northernmost periphery of the species geographic range, to establish unequivocally whether kangaroo rats use torpor in the wild. I capitalized on recent advances in miniature datalogger technology that facilitate implantation of temperature-recording devices in the bodies of small animals (e.g., Mzilikazi et al. 2002, Mzilikazi and Lovegrove 2004). This method provides regular measurements of T_b that support reliable estimates of frequency, depth, duration, and seasonality of torpor, if torpor is used by the animals.

I addressed the following questions regarding thermoregulation of the northernmost kangaroo rats in the field: (i) Does T_b indicate deviations from euthermia that represent torpor? (ii) Do kangaroo rats that use torpor survive the winter? (iii) How often do individuals use torpor? (iv) What proportion of the winter is spent in a torpid state? (v) How deep is torpor according to minimum T_b and is there a seasonal trend in depth of torpor? (vi) What is the duration of torpor episodes and is there a seasonal trend in duration of torpor? (vii) What are the timing and periodicity of torpor episodes? (viii) Do torpor patterns appear to vary substantially between individuals? (ix) Are torpor occurrence, depth, and duration related to environmental factors such as winter air temperature and snow conditions?

Methods

I studied Ord's kangaroo rats in the Middle Sand Hills (50° 35' N 110° 23' W) of southeastern Alberta, Canada, which represents the extreme northernmost periphery of

the species geographic range (Schmidly et al. 1993). This population of kangaroo rats appears to be geographically isolated from the nearest southern conspecifics by at least 350 km, as a relic population that has apparently been segregated for thousands of years (Kenny 1989, Gummer 1995, Gummer 1997) in a region that likely subjects kangaroo rats to more snow and extreme cold temperatures than any locality of other populations in the genus. During my study, there were 181 and 187 days with minimum daily temperature ≤ 0 °C during 2000 and 2001, respectively, at the nearest meteorological station. Similarly there were 91 and 84 days with snow cover during 2000 and 2001, respectively. Overall, the extreme minimum air temperature was -32.8 °C, maximum snow depth was 20 cm, and maximum period of continuous snow cover was 34 d (Environment Canada National Climate Archive 2004).

My study sites were located in Canadian Forces Base Suffield, which includes a Military Training Area and National Wildlife Area, and adjacent rangelands that are primarily used for cattle production and extraction of energy reserves. The majority of the landscape is stabilized sand hills with native scrubland vegetation, including choke cherry (*Prunus virginiana*), sagebrush (*Artemisia cana*), wild rose (*Rosa woodsii*), prickly pear (*Opuntia polyacantha*), sand reed grass (*Calamovilfa longifolia*), and needle and thread (*Stipa comata*). Natural, open sandy habitats are rare in the region, apparently owing to many decades of fire suppression and altered grazing regimes. However, in this area kangaroo rats opportunistically inhabit vehicle trails and graded fireguards where the ground surface has been disturbed by human activities (Gummer 1997, Gummer et al. 1997). These anthropogenic habitats appear to provide adequate open, sparsely vegetated sand that the species requires for its bipedal locomotion and fossorial habits (Bartholomew and Caswell 1951). I surveyed kangaroo rats in anthropogenic habitats by

“nightlighting”, which involves driving a vehicle slowly ($< 30 \text{ km} \cdot \text{h}^{-1}$) with spotlights (10^6 candlepower; Brinkmann, Dallas, Texas) aimed at open sandy areas and edges of vegetation (Kaufman and Kaufman 1982, Gummer 1997, Gummer et al. 1997, Ralls and Eberhardt 1997). Kangaroo rats that were observed by nightlighting were pursued on foot and caught by hand (Gummer 1997, Gummer et al. 1997). I also conducted live-trapping in the vicinity of known kangaroo rat burrows using custom metal live-traps (Sherman-style) baited with rolled oats and equipped with terylene bedding material (Radvanyi 1964).

I conducted nightlighting surveys in October and November in a population of known kangaroo rats from ongoing mark-recapture study (Gummer 1997, Gummer et al. 1997). I recorded the geographic coordinates ($\pm 10 \text{ m}$ Universal Transverse Mercator zone 12, North American Datum 1983) of capture locations using a handheld global positioning system (Garmin 12XL, Olathe, Kansas). Each kangaroo rat was marked with one uniquely numbered metal eartag (Monel 1005-1, National Band and Tag Co., Newport, Kentucky) and a microchip (12 mm Fecava, Avid Canada, Calgary, Alberta) for reliable identification (Williams et al. 1997). The microchip was injected subcutaneously between the scapulae using a sterile 12 gauge needle. I determined the sex of each kangaroo rat and measured body mass ($\pm 1 \text{ g}$) using a spring-scale (Pesola, Switzerland). Individuals with adult body mass ($> 60 \text{ g}$) were selected to undergo surgical implantation of a miniature temperature datalogger (DS1921, iButton ThermoChron, Dallas Semi-conductor, Dallas, Texas; Mzilikazi et al. 2002, Mzilikazi and Lovegrove 2004). Each datalogger was coated with physiologically-compatible wax (paraffin/elvax, Mini-mitter, Sun River, Oregon) and implanted in the peritoneal cavity while the kangaroo rat was anesthetized by IsoFlo (isoflurane, Abott Laboratories,

Saint-Laurent, Quebec) administered from a precision vaporizer. Details of the surgical protocol are reported elsewhere (Chapter 5).

The iButton dataloggers measure 16.3 mm in diameter, 5.9 mm in depth, and weigh 3.3 g (*ca.* 5 % of kangaroo rat body mass). They contain a digital thermometer and clock and they record up to 2048 consecutive time-stamped temperature measurements at a user-defined interval. In addition to the finite number of time-stamped measurements, the dataloggers also record the cumulative total number of temperature measurements in frequency histograms with 2 °C classes. Temperature is measured with an accuracy of 1 °C from –20 to 70 °C and recorded in 0.5 °C increments. The accuracy of the real-time clock is ± 2 min per month from 0 to 45 °C. I programmed dataloggers to record time-stamped T_b measurements once every hour over a period of 85 days. I programmed half of the dataloggers to store time-stamped temperature readings during the first 85 d and the other half of the dataloggers to store time-stamped temperature readings during the most recent 85 d (i.e., overwriting the oldest data with the most recent measurements), in anticipation that some of each type, representing early and late winter, would be recovered. Regardless which 85 d for which the dataloggers stored time-stamped readings, they all recorded cumulative histograms of hourly temperature for the entire winter (November through April).

To facilitate surgical implantation of the dataloggers, kangaroo rats were transported a short distance (*ca.* 10 km) by vehicle to a field station where they were held overnight in small animal cages and provided with bedding material. Surgeries were conducted during the following afternoon. After implantation of the dataloggers, individual kangaroo rats were housed for several more hours to monitor their recovery and then they were transported back to the field sites at night to be released at the exact

location from which they had been caught on the preceding night. Overall, each kangaroo rat was kept in captivity for less than 24 h. Upon their release, I passively followed and observed the behaviour of the implanted kangaroo rats from a short distance (*ca.* 3 to 10 m), using a flashlight, until they fully entered a burrow (Brock and Kelt 2004). The implanted kangaroo rats did not appear to have difficulty with locomotion or navigation: they all promptly maneuvered to burrows. I revisited the same sites during the subsequent spring (March and April) to search for characteristic footprints, tail drags, and open burrows that would indicate that the kangaroo rat had survived the winter. I attempted to recapture the resident kangaroo rats by nightlighting and setting live-traps in the vicinity of active burrows.

The approach of implanting dataloggers in free-living animals for measuring seasonal thermoregulation (Nicol and Andersen 2000, Lehmer et al. 2001, Mzilikazi et al. 2002, Lehmer et al. 2003, Harlow et al. 2004, Mzilikazi and Lovegrove 2004) has the advantage of providing automatic measurements of internal T_b , thereby sampling core T_b at regular intervals and collecting data even when site accessibility, safety for field personnel, and functionality of electronic field equipment (e.g., telemetry equipment) would be limited by extremely cold temperatures and deep snow. Hence this field technique has high potential to contribute significantly to knowledge of natural thermoregulation and torpor in free-living animals under harsh winter conditions (Chapter 5). The datalogger approach also has an inherent risk: it necessitates recovery of animals for acquisition of data. Northern kangaroo rats have low odds of over-winter survival (Gummer 1997), making it difficult to recapture a large proportion of animals for recovery of data. However, the benefit of regular readings throughout winter, which would allow me to address the primary questions of my study, balanced this risk. To

minimize the risk, I attempted to implant 16 kangaroo rats with the expectation of recovering dataloggers from 5 or more individuals in the spring. Unfortunately, mortality during surgeries limited the number of individuals that could be released with implants (Chapter 5). I also planned to cross-reference my findings from the datalogger approach with data from radio telemetry monitoring of a larger number of individual kangaroo rats (Chapter 4, Gummer 1997).

To analyze and interpret the body temperature profiles of implanted kangaroo rats, I needed to adopt an operational definition of torpor. Most torpor studies use an arbitrary threshold temperature in the range of 30 to 37 °C (Hudson 1978, , Lehmer et al. 2001, Barclay et al. 2001, Mzilikazi et al. 2002, Lehmer et al. 2003, Harlow et al. 2004, Mzilikazi and Lovegrove 2004) to identify and quantify torpor bouts. Barclay et al. (2001) recommended using minimum known active temperature (T_{act}) of individuals as the threshold temperature for identification of torpor but I could not quantify minimum T_{act} for the animals in my study because I could not presume which periods of temperature readings represented underground activity or euthermic rest. Barclay et al. (2001) also suggested using the product of depth and duration to quantify torpor, but Willis and Brigham (2003) argued that this was not appropriate given the Arrhenius (Q_{10}) effect that causes incremental reductions in T_b to yield different metabolic savings depending on the particular temperature range (Studier 1981). Willis and Brigham (2003) advocated the continued use of simple arbitrary T_b thresholds to indicate torpor. After consideration of several thresholds (30 to 35 °C), including combination with time (duration) components, and thorough graphical inspection of the data, I made an operational definition of torpor for the purposes of my study where torpor was defined by $T_b < 33$ °C for at least 2 consecutive measurements (2 h). I thereby excluded many

episodes that would otherwise have appeared as shallow torpor < 2 h, some of which were probably spurious and caused by the relative accuracy of the datalogger measurements. By definition, this approach is conservative and would likely result in underestimation of the frequency of short-term, shallow deviations from euthermia.

I estimated ambient temperature (T_a) conditions by recording hourly measurements of soil temperature at 1 m depth belowground at a randomly selected site near the centre of my study area. Soil temperature was measured using an automatic datalogger (Campbell Scientific 21X, Edmonton, Alberta) equipped with a PVC insulated copper-constantan (type T; ± 1 °C) thermocouple. Ord's kangaroo rats have been found to occupy burrows from 0.2 to 0.7 m soil depths in more southern localities (southeastern Idaho; Reynolds and Watakin 1987) and I previously excavated burrows of up to 1 m depth in my study area. Unfortunately, the thermocouple wires were destroyed by coyotes (*Canis latrans*) during 2001 and hence the soil temperature data were only available for the first winter of my study (2000/2001). I also obtained daily and hourly weather data, describing air temperature and snow depth, from the Environment Canada National Climate Archive (2004) for the meteorological station at Medicine Hat Airport (50° 35' N 110° 23' W) which is located approximately 68 km south-southwest of the centre of my study area.

I quantified deviations from euthermia and estimated frequency of torpor by determining the number of torpor episodes and number of days on which each kangaroo rat exhibited torpor. I also estimated the cumulative amount of time and proportion of the winter that was spent in a torpid state according to the overall frequency distributions of hourly T_b . I used Kolmogorov-Smirnov two sample tests (Sokal and Rohlf 1995) to compare the frequency distributions of hourly T_b . I compared the overall frequency

distributions of hourly T_b between individual kangaroo rats and I also compared the early winter (first 85 d) and late winter (last 85 d) frequency distributions between kangaroo rats. Within each kangaroo rat, I tested whether the frequency distributions of hourly T_b differed between early and late winter periods. For these tests on the frequency distributions of hourly T_b , the assumption of independence of observations was likely not met. Therefore, in any cases where I rejected the null hypothesis that the frequency distributions were similar, I also reported the hypothetical, minimum required sample size (as n_1 and n_2) for which the observed effect (maximum unsigned difference between the relative cumulative frequency distributions) would still have caused rejection of the null hypothesis at the $\alpha = 0.05$ level.

None of the variables describing torpor had symmetrical frequency distributions. Therefore, I described the details of torpor of each kangaroo rat using the median, minimum, and maximum values. Although the majority of comparative studies of torpor evaluate torpor characteristics according to arithmetic means and standard errors (e.g., Geiser and Ruf 1995), I did not report these descriptive statistics because they would not have been representative of the torpor patterns that I documented.

I quantified depth of torpor by determining the minimum recorded T_b for each torpor episode. I estimated duration of torpor by determining the number of hours between entry and arousal, where entry was defined as the time of day of the last hourly reading with $T_b \geq 33$ °C prior to torpor and arousal was defined as the time of day of the first $T_b \geq 33$ °C after torpor. To explore whether there were seasonal trends in depth and duration of torpor for each individual kangaroo rat, I used autoregression to estimate linear and curvi-linear (quadratic) models with first order autoregressive errors for each kangaroo rat. I used Akaike's Information Criterion (AIC; Burnham and Anderson

2002) scores to determine whether linear or curvi-linear functions represented better models of seasonal trends in depth or duration of torpor. In cases where I did not find depth or duration of torpor to be autocorrelated, I applied standard linear regressions to evaluate the potential relationships between depth/duration of torpor and torpor episode number. In some cases, the data appeared to be heteroscedastic and therefore I also reported the more conservative Spearman rank-order correlation of depth/duration of torpor and torpor episode number.

To explore the potential relationships between torpor and daily air temperature and snow conditions, I used autoregression to estimate linear and logistic regression models with first order autoregressive errors (Harlow et al. 2004). Daily snow depth data were log-transformed to convert the positively skewed frequency distribution into a more symmetrical one (Krebs 1989). I expected that both daily minimum temperature and snow depth were likely to contribute to torpor occurrence, depth, and duration. However, given that daily minimum temperature and snow depth were negatively correlated, I estimated separate regression models for each variable to avoid the potentially confounding effects of multi-collinearity (Zar 1999). I performed logistic autoregression to evaluate whether the probability of torpor by an individual kangaroo rat was related to daily minimum air temperature and snow depth (log-transformed). Similarly, for each individual I used linear autoregression to examine whether torpor depth and duration were related to daily minimum air temperature and snow depth (log-transformed). In instances where I did not find significant autocorrelation terms, I proceeded to apply standard regression models.

Results

I successfully implanted and released eight kangaroo rats during late autumn (five in October 2000 and three in November 2001) and I recaptured and recovered dataloggers from two kangaroo rats that survived winter: one adult male was recaptured in April 2001 and one adult female was recaptured in April 2002. Neither of the two kangaroo rats had lost any body mass over the course of the winter. The thermoregulation profiles (Fig. 3.1) and overall frequency histograms (Fig. 3.2) of the implanted kangaroo rats illustrated that they both used torpor, but to varying extents. During the period of time-stamped T_b measurements, the two kangaroo rats used daily torpor on 38 and 27 occasions, respectively. Torpor was occasionally used more than once on a given day (Fig. 3.3). One kangaroo rat entered torpor on 34 of 85 days whereas the second kangaroo rat exhibited torpor on 25 of 85 days. Table 3.1 provides a summary of the details of torpor use for the kangaroo rats from which I recovered thermoregulation data.

The overall frequency histogram of T_b for the first kangaroo rat represented 3783 hourly measurements and the frequency histogram for the second kangaroo rat was based on 4029 hourly measurements. These frequency histograms indicated very different thermoregulation patterns from November through April (Fig. 3.2; $D = 0.444$, $P < 0.05$, $n_1 = 42$ and $n_2 = 45$). Similarly, the frequency distributions of hourly T_b also differed between individuals when comparing strictly the early winter ($D = 0.289$, $P < 0.05$, $n_1 = 93$ and $n_2 = 110$) and late winter ($D = 0.601$, $P < 0.05$, $n_1 = 24$ and $n_2 = 23$) periods. Cumulatively, the first kangaroo rat spent approximately 872 h (23 %) of the winter in a torpid state whereas the other kangaroo rat spent approximately 148 h (4 %) of the winter in a torpid state. The frequency distributions of hourly T_b indicated that the

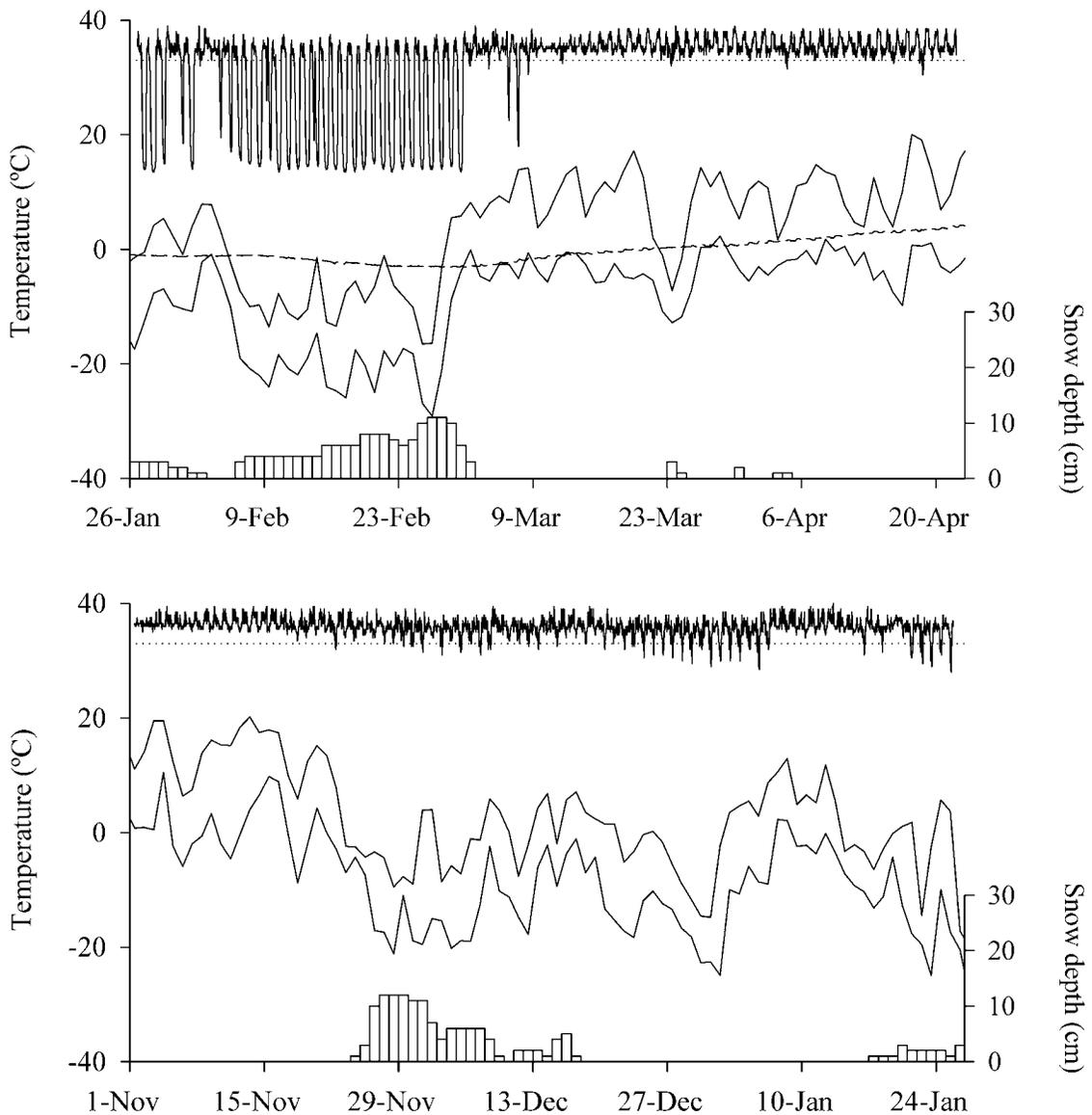


Figure 3.1 Thermoregulation profiles of two free-living Ord's kangaroo rats according to hourly measurements of body temperature (T_b) at the northernmost periphery of the species geographic range. The top graph represents thermoregulation of a male kangaroo rat in late winter (2001) whereas the bottom graph shows thermoregulation by a female in early winter (2001/2002). For each graph, the upper solid line represents T_b , the two middle solid lines are daily maximum and minimum air temperatures, the short dashed line is soil temperature at 1 m depth, and the vertical bars indicate daily snow depth (on the secondary ordinate). Daily air temperature and snow depth data were obtained from the Environment Canada National Climate Data Archive (2004). Periods with $T_b < 33$ °C (dotted line) for at least 2 h were considered to represent torpor.

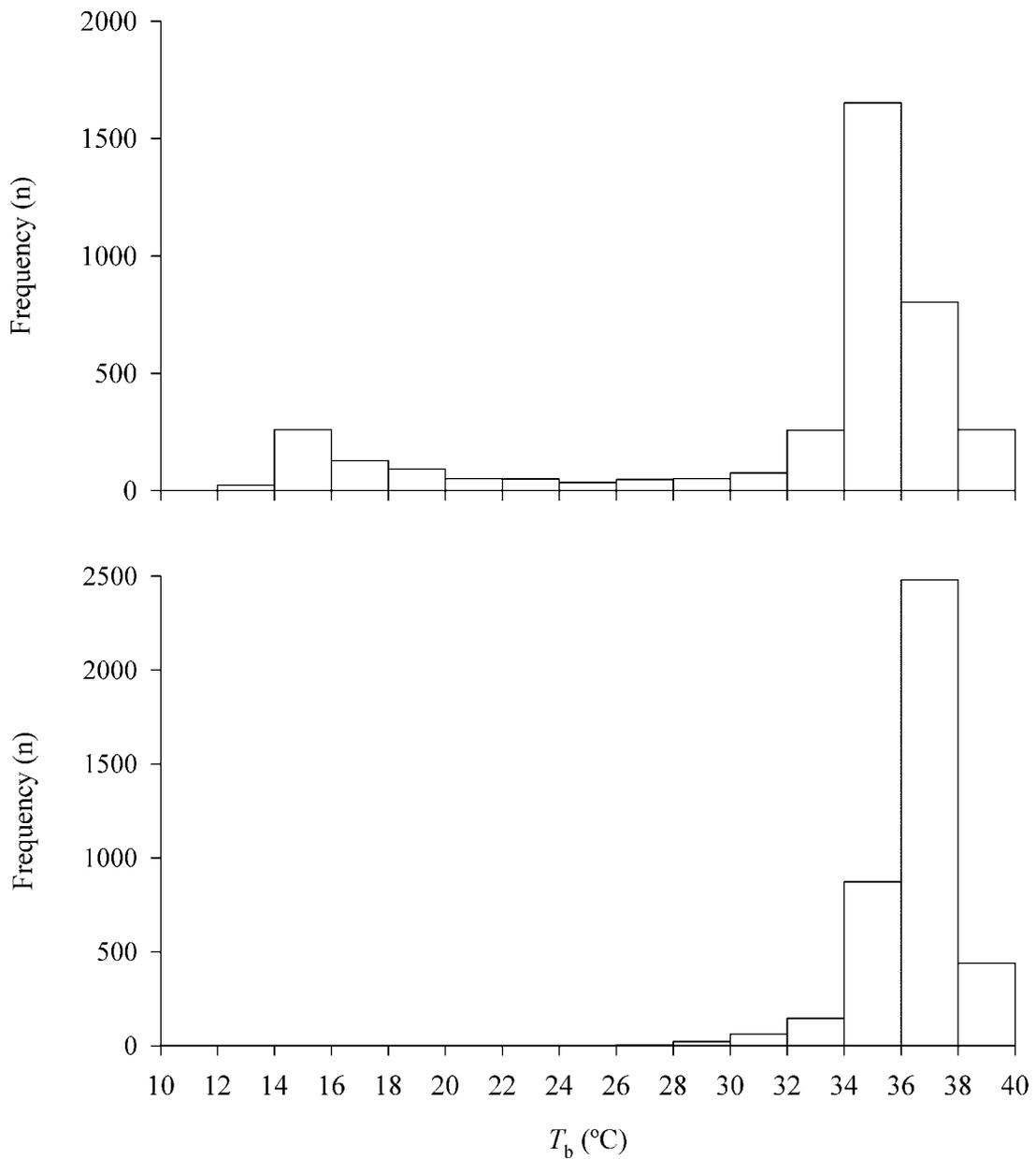


Figure 3.2 Frequency histograms of hourly measurements of body temperature (T_b) of two free-living Ord's kangaroo rats during winter (November through April) at the northernmost periphery of the species geographic range. The top graph corresponds to a male kangaroo rat (2000/2001) whereas the bottom graph represents a female kangaroo rat (2001/2002).

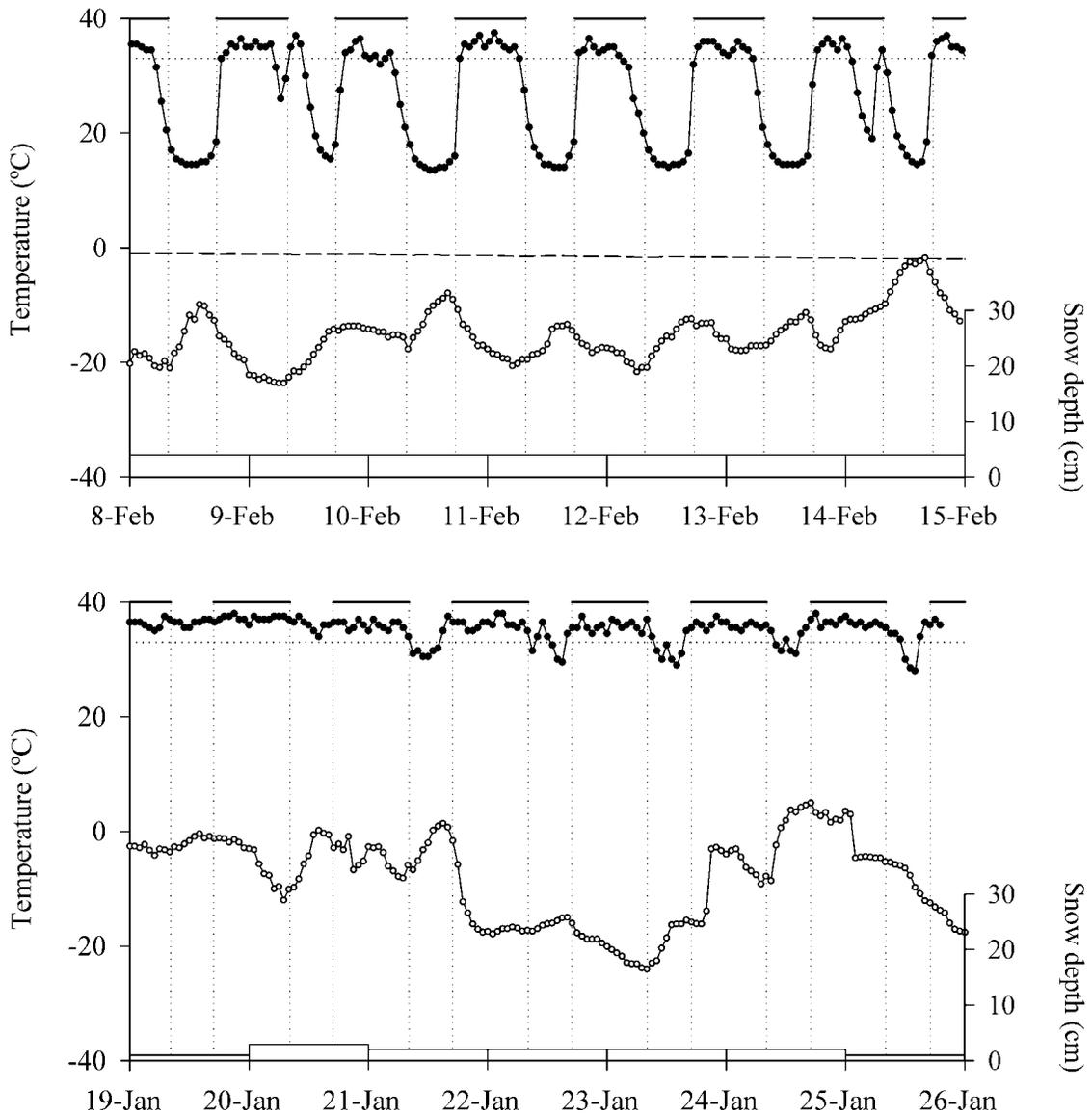


Figure 3.3 Thermoregulation profiles of two free-living Ord's kangaroo rats according to hourly measurements of body temperature (T_b) at the northernmost periphery of the species geographic range. The top graph represents thermoregulation of a male kangaroo rat (2001) whereas the bottom graph shows thermoregulation by a female (2002). For each graph, the solid line with black circles represents hourly T_b , the horizontal solid bars indicate nighttime hours with vertical dotted lines to indicate sunrise and sunset, the solid lines with the open circles represent hourly air temperature, the long dashed line is soil temperature at 1 m depth, and the vertical bars indicate daily snow depth (on the secondary ordinate). Hourly air temperature and daily snow depth data were obtained from the Environment Canada National Climate Data Archive (2004). Periods with $T_b < 33$ °C (horizontal dotted line) for at least 2 h were considered to represent torpor.

Table 3.1 Details of winter torpor in two free-living Ord's kangaroo rats at the northernmost periphery of the species geographic range.

| | Male 2000/2001 | | | Female 2001/2002 | | |
|--------------------------------------|----------------|---------|---------|------------------|---------|---------|
| | Median | Minimum | Maximum | Median | Minimum | Maximum |
| Minimum T_b (°C) | 14.5 | 13.5 | 32.0 | 31.0 | 27.5 | 32.0 |
| Duration (h) | 13.0 | 3.0 | 17.0 | 4.0 | 3.0 | 7.0 |
| Entry time (h:mm) | 4:00 | 0:00 | 12:00 | 12:00 | 8:00 | 13:00 |
| Entry rate (°C · h ⁻¹) | 6.0 | 2.5 | 7.0 | 3.0 | 2.0 | 4.0 |
| Arousal time (h:mm) | 16:30 | 11:00 | 19:00 | 15:00 | 13:00 | 16:00 |
| Arousal rate (°C · h ⁻¹) | 14.5 | 3.0 | 18.0 | 3.0 | 2.0 | 6.0 |

first kangaroo rat spent comparable amounts of time in various temperature states during early and late winter ($D = 0.0544$, $P = 0.2$) but that the second kangaroo rat did not ($D = 0.289$, $P < 0.05$, $n_1 = 100$ and $n_2 = 103$). The frequency distribution of late winter thermoregulation of the second kangaroo rat was more leptokurtic and slightly more negatively skewed than the frequency distribution of its early winter thermoregulation (Fig. 3.4). Based on the overall frequency distributions of T_b , I estimated that the 2 kangaroo rats used torpor on approximately 75 and 38 occasions, respectively.

One kangaroo rat used much deeper and longer torpor episodes than the other kangaroo rat (Table 3.1). Both individuals exhibited slightly negative, seasonal trends in minimum T_b on subsequent torpor bouts, although the final few torpor bouts were more shallow for one kangaroo rat that was monitored during late winter and early spring (Fig. 3.5). The seasonal trend in minimum T_b therefore approximated a quadratic function for one individual (Fig. 3.5; $F_{[2,31]} = 15.89$, $P < 0.001$) and a linear relationship for the other kangaroo rat ($F_{[1,24]} = 9.238$, $P = 0.006$, $r_s = -0.516$, $P = 0.004$). Similarly, both individuals showed seasonal increases in maximum duration of torpor, although the final few torpor bouts were of shorter duration for the individual that was monitored during late winter and early spring (Fig. 3.6). Therefore the seasonal trend in duration of torpor also approximated a quadratic function for one individual (Fig. 3.6; $F_{[2,31]} = 8.90$, $P = 0.001$) and a linear relationship for the other kangaroo rat ($F_{[1,24]} = 4.264$, $P = 0.05$, $r_s = 0.335$, $P = 0.05$).

The two kangaroo rats used torpor primarily during pre-dawn and daylight hours: arousal from torpor was approximately coincident with sunset (Table 3.1, Fig. 3.3). For the first kangaroo rat, which used the deepest and longest torpor episodes, the rate of

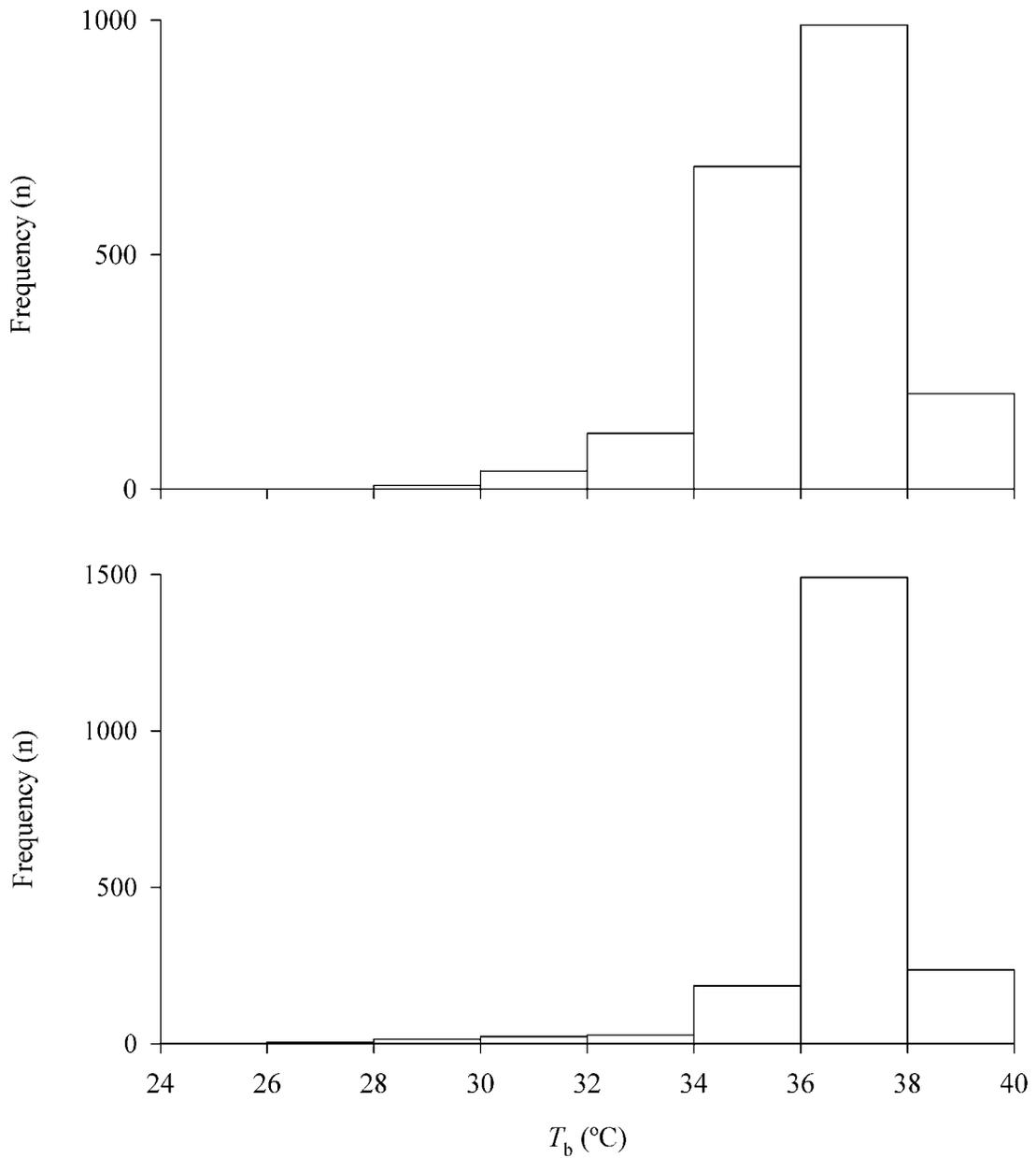


Figure 3.4 Frequency histograms of hourly measurements of body temperature (T_b) of a free-living, female Ord's kangaroo rat during early winter (1-Nov-2001 to 25-Jan-2002; top graph) and late winter (26-Jan-2002 to 18-Apr-2002; bottom graph).

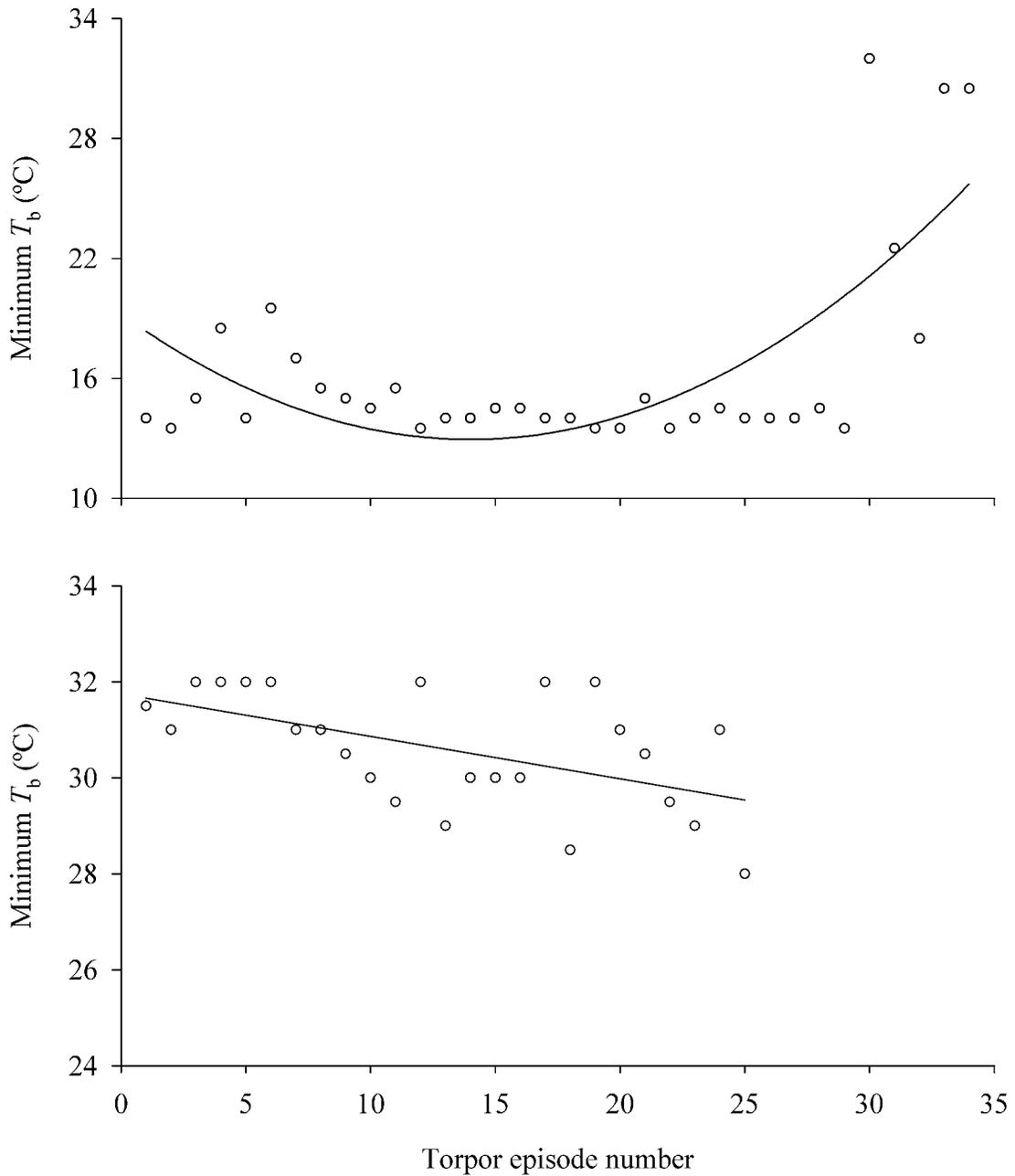


Figure 3.5 Seasonal trends in depth of torpor (minimum T_b) of two free-living Ord's kangaroo rats at the northernmost periphery of the species geographic range. The top graph corresponds to a male kangaroo rat during late winter (2000/2001; [Minimum T_b] = $19.2 - 0.895[\text{Episode}] + 0.032[\text{Episode}]^2$) whereas the bottom graph represents a female kangaroo rat during early winter (2001/2002; ([Minimum T_b] = $31.8 - 0.088[\text{Episode}]$)).

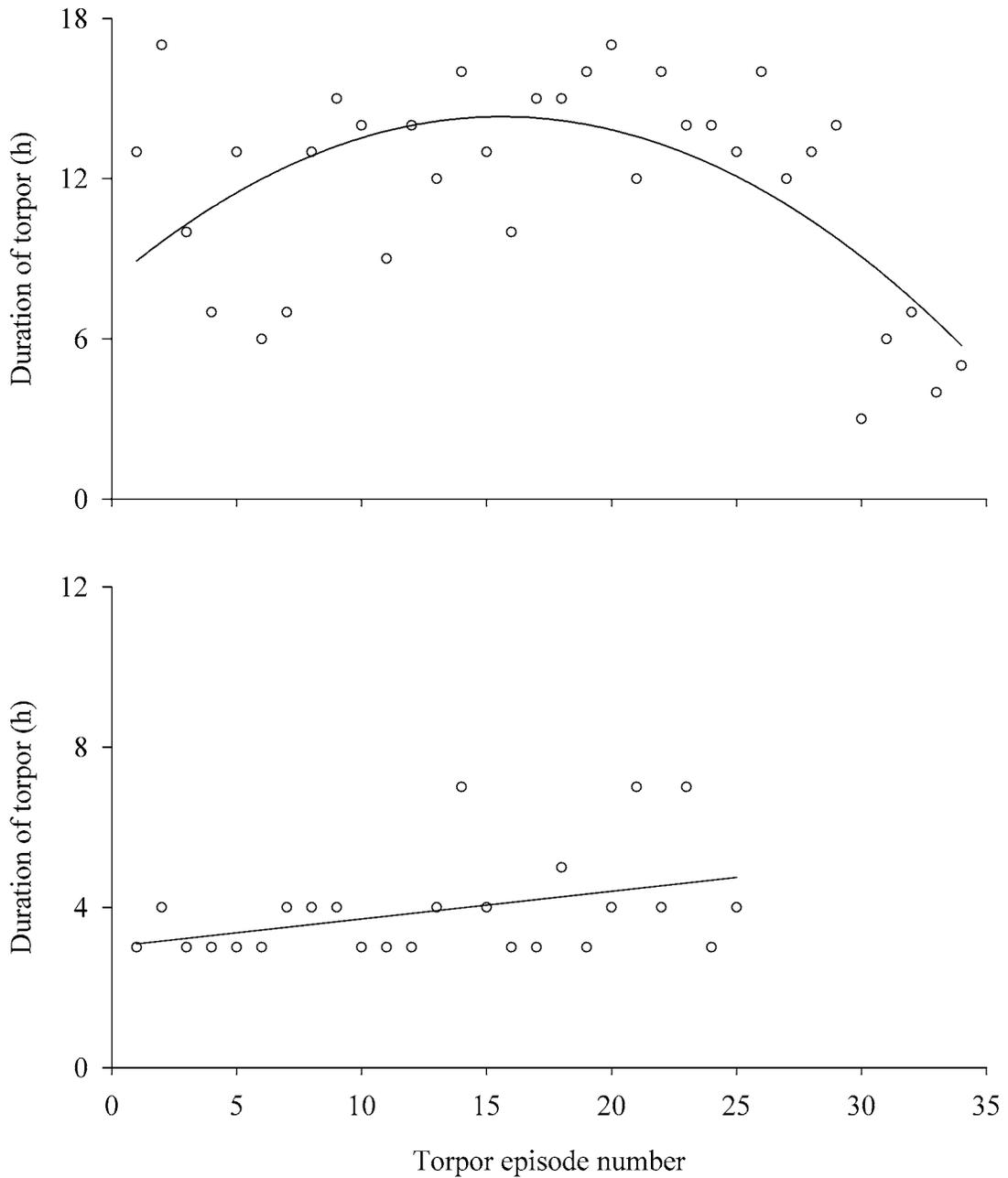


Figure 3.6 Seasonal trends in duration of torpor of two free-living Ord's kangaroo rats at the northernmost periphery of the species geographic range. The top graph corresponds to a male kangaroo rat during late winter (2000/2001; $[\text{Duration}] = 8.16 + 0.790[\text{Episode}] - 0.025[\text{Episode}]^2$) whereas the bottom graph represents a female kangaroo rat during early winter (2001/2002; $[\text{Duration}] = 3.02 + 0.069[\text{Episode}]$).

change of T_b was much higher during arousal from torpor than for torpor entry (Table 3.1). Overall, the median periodicity of torpor for both kangaroo rats was precisely 24 h. Torpor was observed during every month from November through April. Both kangaroo rats used torpor during periods of freezing air temperatures and snow cover, though not exclusively (Figs. 3.7 and 3.8). I found that probability of torpor on a given day was negatively related to daily minimum air temperature for each kangaroo rat (Fig. 3.7; $\chi^2 = 22.843$, $df = 1$, $P < 0.001$ and $\chi^2 = 14.165$, $df = 1$, $P < 0.001$). Probability of torpor was positively related to snow depth for only the first of the two kangaroo rats (Fig. 3.8; $\chi^2 = 28.593$, $df = 1$, $P < 0.001$ and $\chi^2 = 0.378$, $df = 1$, $P = 0.539$). Similarly, torpor depth and duration of the first kangaroo rat were both related to daily minimum air temperature ($F_{[1,33]} = 27.541$, $P < 0.001$ and $F_{[1,33]} = 29.137$, $P < 0.001$) and snow depth ($F_{[1,33]} = 19.949$, $P < 0.001$ and $F_{[1,33]} = 36.954$, $P < 0.001$). Depth and duration of torpor of the second kangaroo rat were related to daily minimum air temperature ($F_{[1,24]} = 4.925$, $P = 0.037$ and $F_{[1,24]} = 6.475$, $P = 0.018$) but were not related to snow depth ($F_{[1,24]} = 0.206$, $P = 0.654$ and $F_{[1,24]} = 0.163$, $P = 0.690$). On the 34 days that torpor was used for which soil temperature data were available, soil temperature at 1 m depth belowground ranged between -3.1 and 3.3 °C, with a mean (\pm standard deviation) temperature of -1.8 ± 1.2 °C.

Discussion

My findings represent the first unequivocal documentation of winter thermoregulation and torpor in free-living kangaroo rats of any species. Contrary to the suggestions of previous authors (MacMillen 1983, French 1993), it is now apparent that

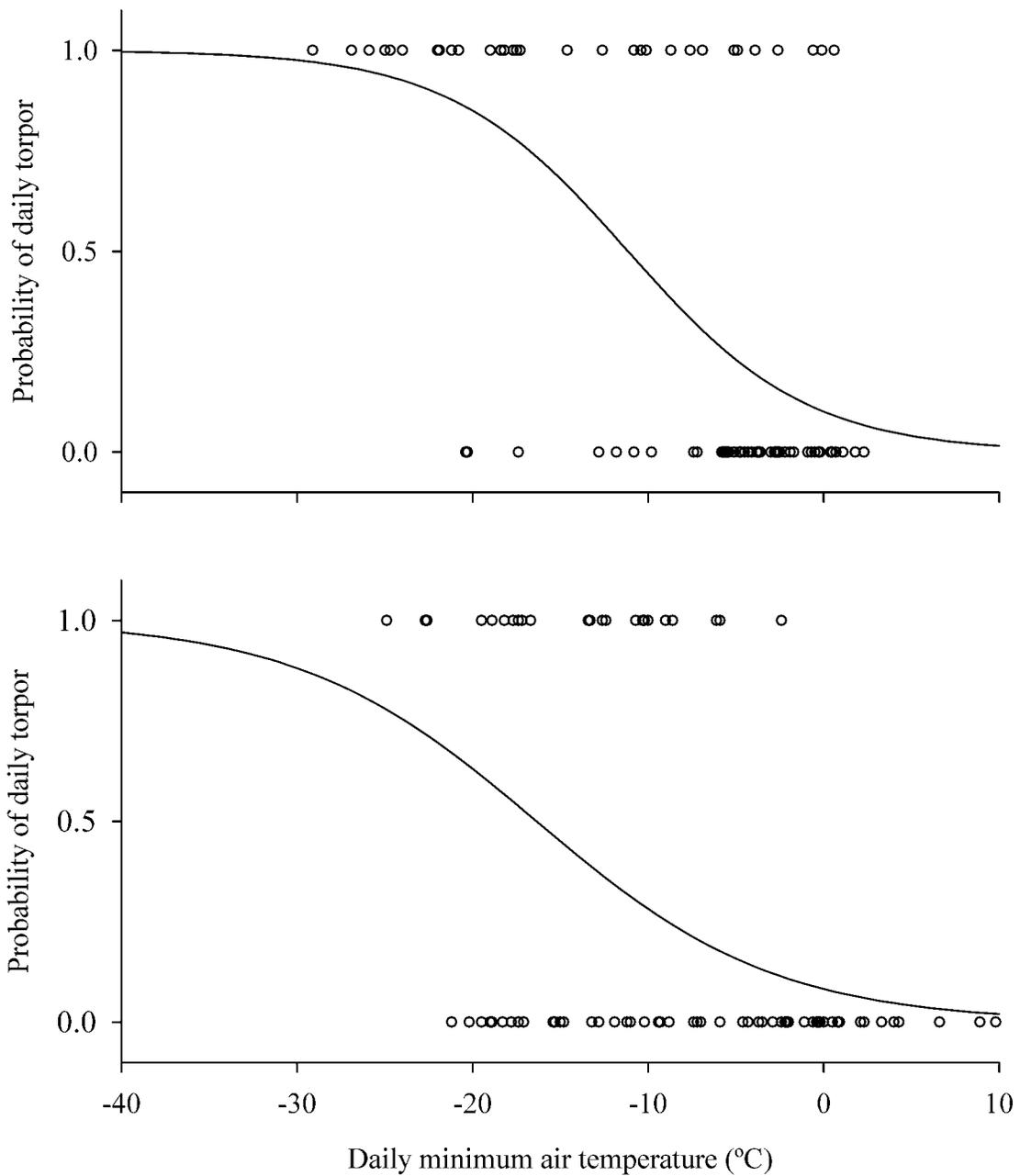


Figure 3.7 Binary logistic regression of probability of daily torpor with daily minimum air temperature for two free-living Ord's kangaroo rats at the northernmost periphery of the species geographic range. The top graph corresponds to a male kangaroo rat during late winter (2000/2001) whereas the bottom graph represents a female kangaroo rat during early winter (2001/2002).

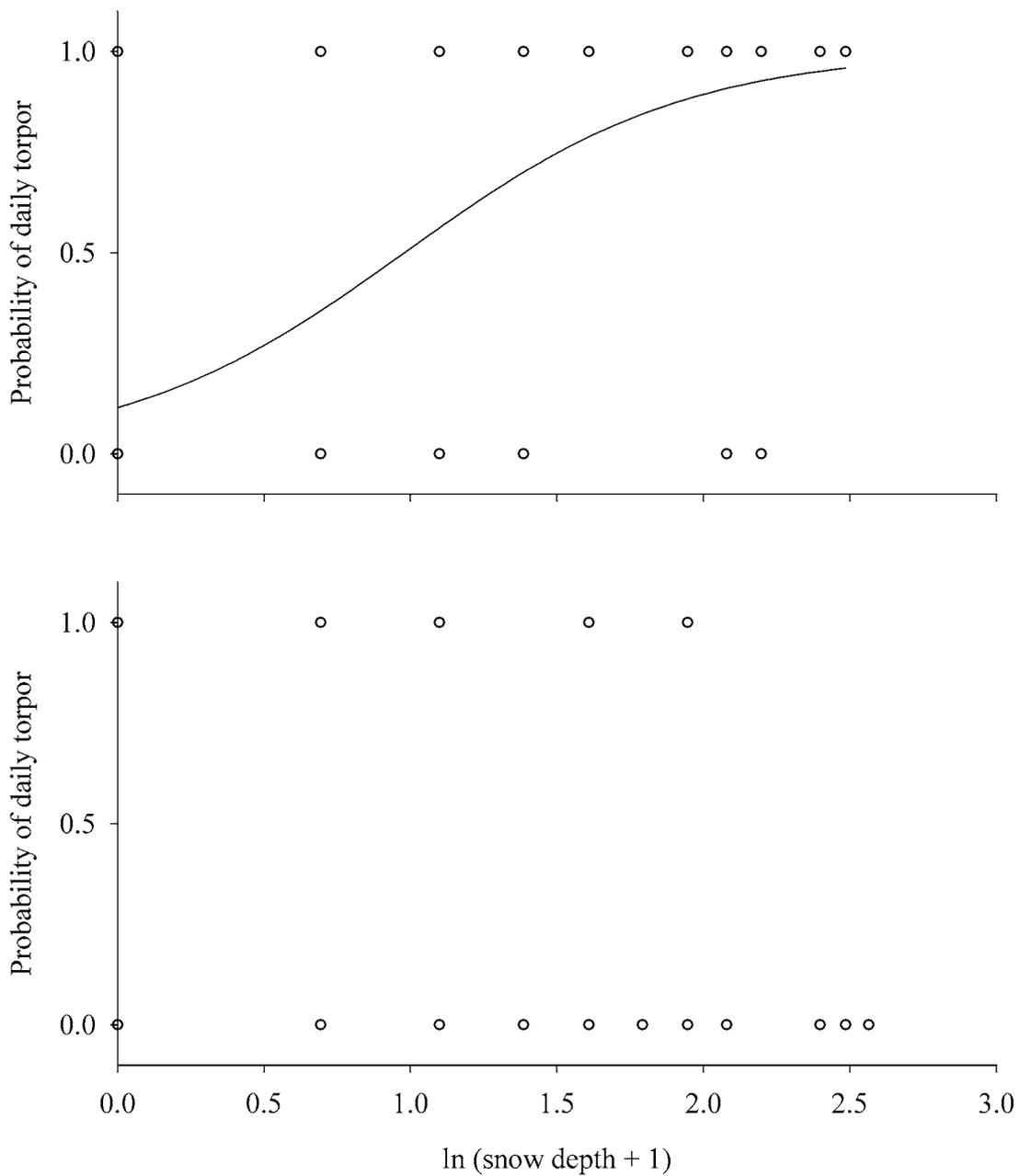


Figure 3.8 Binary logistic regression of probability of daily torpor with daily snow depth (log-transformed) for two free-living Ord's kangaroo rats at the northernmost periphery of the species geographic range. The top graph corresponds to a male kangaroo rat during late winter (2000/2001) whereas the bottom graph represents a female kangaroo rat during early winter (2001/2002). The fitted curve is not shown on the bottom graph because this binary logistic regression was not found to be significant.

the capability of torpor is well developed in kangaroo rats—at least in the northernmost population of the genus. Northern Ord’s kangaroo rats use repetitive, daily torpor episodes, with minimum T_b as low as 13.5 °C and duration of up to 17 h during winter periods of cold temperatures and deep snow. Hence, torpor is clearly an ecologically significant over-winter strategy of the northernmost kangaroo rats. The extent to which other populations or species of the genus may use torpor remains to be determined and could be elucidated by systematic field studies using similar techniques as those documented herein.

The thermoregulation data that I obtained from free-living kangaroo rats indicated a large number of torpor bouts but from only two individual kangaroo rats and each in different years. As such, my findings need to be interpreted cautiously. Potential differences between individuals, sexes, or years cannot be inferred from these results exclusively. Similarly, I cannot extrapolate from my findings to predict the potential thermoregulatory responses of northern kangaroo rats to particular ambient weather conditions. Yet, my findings address a major gap in understanding of the physiological ecology of kangaroo rats under natural field conditions. To my knowledge, my results represent the first reliable documentation of torpor bouts and natural thermoregulation patterns in kangaroo rats in the field. Previous radio telemetry efforts yielded only 20 suspected torpor bouts from seven kangaroo rats according to external measurements of T_{sk} (Gummer 1997). In comparison, the resultant T_b measurements from the dataloggers carried by two kangaroo rats of this study allowed me to estimate a total of 113 torpor bouts, of which 65 torpor episodes were documented with hourly time-stamped T_b measurements that facilitated in-depth evaluation of torpor depth, duration, entry, and arousal. It is also important to note that my results are entirely consistent with new

(Chapter 4) and previous (Gummer 1997) results from radio telemetry that indicate that kangaroo rats use torpor on a daily basis during winter. Hence, although the specific number of individuals of my current study is small, it is corroborated by other findings from additional animals and independent field methods. Cumulatively, these studies provide a more complete understanding of winter thermoregulation and torpor patterns in the northernmost kangaroo rats.

Hourly measurements of T_b of kangaroo rats revealed many substantial deviations from euthermy that represented torpor. However I also estimated many more shallow torpor episodes, particularly for the second kangaroo rat, according to the operational definition of torpor that I used ($T_b < 33$ °C for at least 2 h). Although many researchers have used a lower threshold T_b (e.g., 30 or 31 °C; Hudson 1978, Barclay et al. 2001, Lehmer et al. 2003) and some have used a higher threshold T_b (e.g., 36 or 37 °C; Barclay et al. 2001, Lehmer et al. 2001, Lehmer et al. 2003, Harlow et al. 2004) to quantify various aspects of torpor, I consider that 33 °C was an appropriate threshold T_b below which to infer torpor in kangaroo rats. It was likely to provide conservative estimates of torpor frequency and duration because 33 °C is much lower than the resting euthermy T_b reported for Ord's kangaroo rats held at 5 °C in captivity (37 ± 0.3 °C; Wunder 1974). Furthermore, by incorporating a duration component (> 2 h) in my operational definition of torpor, I presumably excluded some erroneous T_b measurements but I also established a bias against short-term, shallow torpor episodes. There are obviously pros and cons associated with any particular threshold that is applied more or less arbitrarily. Yet I could have used any other of the common thresholds (30 to 37 °C) to indicate torpor and the primary conclusions and implications of my study would have remained the same. Regardless of the particular threshold

temperature/duration, it is clear that T_b of kangaroo rats declined well below any of the threshold T_b 's that are typically used to indicate torpor (Barclay et al. 2001). Kangaroo rats undoubtedly use daily torpor during winter at the northern periphery of the species geographic range.

According to my current findings, as well as radio telemetry studies of kangaroo rats' T_{sk} (Gummer 1997, Chapter 4), it appears that some individual kangaroo rats do not use deep bouts of torpor. Relatively shallow deviations in T_b may be relied upon by some individuals to accomplish moderate conservation of metabolic resources (Webb et al. 1993). It would be useful for future studies to attempt to document the minimum T_{act} (Barclay et al. 2001) of individual kangaroo rats by studying implanted kangaroo rats that are held temporarily in captivity, in an effort that the operational definition of torpor could potentially be refined to better identify and quantify even the most shallow deviations from euthermia.

The datalogger method that I used to document thermoregulation of free-living kangaroo rats necessitated that individuals survived the winter to be included in the results of my study. Therefore, it is clear that kangaroo rats that use torpor are capable of surviving the winter. Importantly, this excludes the possibility that torpor is used by kangaroo rats only as they die from starvation (Dawson 1955, Carpenter 1966, Yousef and Dill 1971, Breyen et al. 1973, MacMillen 1983, French 1993). The kangaroo rats of my study presumably were not starving because they should have had access to whatever natural, pre-winter food caches that they had accumulated in their underground burrows. Furthermore, the kangaroo rats that were recaptured in early spring had not lost body mass in comparison with their autumn body mass. They also survived the extended winter period despite frequent torpor bouts over the course of approximately 160 days;

clearly then, they were not facing imminent death from starvation, winter conditions, or potential wounds/infection from the surgical procedure. In contrast, Carpenter (1966) reported that Merriam's kangaroo rats did not enter torpor in laboratory trials until they had been starved to the point that their body mass dropped substantially (17 to 21 %), and then they used daily torpor for only 4 to 6 days after which the cycles of torpor always ended in death of the animals. I can confidently conclude that the torpor that I documented in the northernmost Ord's kangaroo rats is fundamentally different than the patterns of torpor that have been documented in laboratory studies of starving, dying kangaroo rats (Dawson 1955, Carpenter 1966, Yousef and Dill 1971, Breyen et al. 1973).

Northern Ord's kangaroo rats use torpor on a daily basis during winter, as had been suggested by radio telemetry studies of T_{sk} (Gummer 1997, Chapter 4). They spend a considerable amount of the winter in a torpid state, up to 25 % of time from November through April. Conversely, they spend more than 75 % of the winter in a euthermic state, but they apparently do not emerge from their underground burrows during periods of continuous snow cover (Gummer 1997). The extent to which they remain euthermic underground during winter is not surprising because kangaroo rats store large quantities of food in their burrows (Herrera et al. 2004). They are among the leanest mammals (Schreiber and Johnson 1975) and presumably need to continually replenish metabolic resources throughout the winter to facilitate thermogenesis. Generally animals that use torpor are categorized as either fat-storing or food-storing hibernators (Humphries et al. 2001). Given that kangaroo rats are now known to use torpor under natural conditions, and they store large amounts of food in their underground burrows, they should be considered food-storing hibernators. Food-storing hibernators typically exhibit relatively

shallow torpor of shorter duration, and with longer periods of euthermy, compared to fat-storing hibernators (Humphries et al. 2001). The extended periods of euthermy that characterize thermoregulation patterns of food-storing hibernators may reflect the need for the animals to load enough food into the gut to cover the metabolic requirements of the next torpor bout (Humphries et al. 2001).

The maximum depth of torpor (minimum T_b) that I recorded in kangaroo rats, 13.5 °C, is slightly lower than the arbitrary threshold of 15 °C that is commonly used to define deep torpor (French 1993). The kangaroo rats of this study maintained T_b at least 10 to 16 °C above T_a of the soil at 1 m depth, which was frozen on average. Maximum depth of torpor as determined from implanted dataloggers was comparable to minimum T_{sk} recorded by radio telemetry of 13 °C (Chapter 4) and 17 °C (Gummer 1997). These findings were similar to the minimum T_b of 16 to 18 °C among starving and dying, torpid Merriam's kangaroo rats (Carpenter 1966) and panamint kangaroo rats (Dawson 1955). However, depth of torpor of northern kangaroo rats is not as low as that documented for kangaroo mice and pocket mice in captivity (2 to 6 °C; Bartholomew and MacMillen 1961, Meehan 1977). Torpid kangaroo mice have been found to have esophageal temperatures from 1.0 to 3.5 °C above T_a (Brown and Bartholomew 1969).

There was a gradual trend towards increased depth of torpor on subsequent torpor bouts, with the exception that the late winter and early spring torpor of one kangaroo rat tended to be much more shallow. A general seasonal decline in minimum T_b is expected as soil and aboveground air temperatures generally become progressively colder for much of the winter season. As well, it is likely that kangaroo rats' underground food stores become depleted during mid- to late winter, which may cause individuals to adopt deeper torpor to conserve more metabolic resources. Later in the

year, the early spring trend that one kangaroo rat exhibited towards more shallow torpor may have reflected an increase in the general availability of new food resources due to the scarcity of snow. To my knowledge, no previous studies have reported whether there are gradual seasonal trends in the depth of torpor of any heteromyid rodents, in captivity or otherwise.

Duration of torpor bouts of kangaroo rats was always < 24 h and therefore it should be categorized as daily torpor rather than hibernation, according to the classification of Geiser and Ruf (1995). The maximum duration (17 h) that I observed was much longer than estimates of maximum torpor duration by radio telemetry: 7 h (Chapter 4) and 8.25 h (Gummer 1997). This apparent discrepancy is likely a function of differences between field techniques, seasonality of observations, and operational definitions of torpor. For example, the gradual trend towards increased depth and duration of torpor necessitates that mid- to late winter torpor episodes should, on average, represent torpor bouts of the longest duration for any one individual. Yet radio telemetry methods are constrained to early winter observations of T_{sk} due to transmitter battery-life limitations. Hence radio telemetry is only likely to detect the shortest torpor bouts, on average (Gummer 1997, Chapter 4). I found no previous studies that explicitly reported the duration of torpor bouts of captive kangaroo rats. Captive kangaroo mice held at low T_a with restricted food rations exhibit torpor duration ranging from 7 h to 3.5 d (Brown and Bartholomew 1969) and pocket mice have been reported to exhibit hibernation cycles of up to 8 d in duration (Meehan 1977).

Kangaroo rats exhibited a slight seasonal trend towards increasing duration of torpor on subsequent torpor bouts, with the exception that the late winter and early spring torpor of one kangaroo rat tended to have much shorter duration. Such seasonal

trends in duration of torpor are common among species that use daily torpor and seasonal hibernation (French 1986). For kangaroo rats, one potential contributing factor to the trend towards increasing duration of torpor may be gradual depletion of underground food caches over the course of the winter. Captive kangaroo mice and pocket mice on reduced food rations have been found to match the time that they spend in torpor to their daily energetic deficit (Tucker 1966, Brown and Bartholomew 1969, Wolff and Bateman 1978, French 1993). Although I did not document any multi-day torpor bouts in kangaroo rats, kangaroo mice and pocket mice gradually extend their daily torpor into hibernation cycles (Browner and Cade 1971, French 1977). Other food-storing species that use torpor typically exhibit torpor episodes with maximum duration > 24 h as well (Humphries et al. 2001). It is possible that kangaroo rats may also use multi-day torpor episodes in some circumstances, and future studies on a larger number of kangaroo rats, or across multiple years with varying conditions, may reveal these patterns. For example, some kangaroo rats may enter more long-term hibernation cycles during particularly long and cold winters, or if they inhabit sites where diet or microclimate considerations either facilitate, or necessitate, more intensive torpor.

The timing of torpor and euthermy among kangaroo rats reflects their typical (nocturnal) activity patterns, with entry into torpor generally occurring during the pre-dawn or morning periods and arousal from torpor in the afternoon. Arousal is generally associated with sunset. These findings are congruent with the circadian timing of daily torpor for many other nocturnal species. Overall, the periodicity of daily torpor was precisely 24 h, suggesting that kangaroo rats experience circadian cues such as photoperiod, to maintain the precise periodicity of circadian activity patterns. During euthermic activity periods, kangaroo rats may venture near to surface exits of their

burrows where there may be evidence of ambient light conditions, but there is no evidence that they dig through or emerge from the snow (Chapter 4, Gummer 1997). Previous findings in captivity indicated that kangaroo rats used torpor primarily during the light phase of the photoperiod (Carpenter 1966); similar findings have been reported for kangaroo mice and pocket mice (Brown and Bartholomew 1969, French 1977). Brown and Bartholomew (1969:709) noted that “under natural conditions such a timing of arousal would afford maximal conservation of energy and a maximum nocturnal period for foraging.”

The relatively deep torpor bouts exhibited by one kangaroo rat in my study provided good opportunity to document its rate of entry and arousal from torpor over a relatively wide range of T_b . Its entry into torpor was much slower than arousal rate. The maximum re-warming rate during arousal ($18\text{ }^\circ\text{C} \cdot \text{h}^{-1}$) shows a high capacity for thermogenesis. Entry into torpor is accomplished by passive heat loss, which is therefore relatively slow, compared to arousal from torpor which is achieved by active thermogenesis. Rates of entry into torpor and arousal from torpor have not been well documented in kangaroo rats, even in studies of captive animals. In most previous studies of captive heteromyids, torpid individuals were removed from low T_a and allowed to re-warm at room temperature, which would promote heating from passive, exogenous sources (Dawson 1955, Carpenter 1966, Yousef and Dill 1971, Hudson 1978). The fact that starving kangaroo rats die during arousal even when they are moved to a T_a of 27 to 30 °C where passive heating could assist in their arousal is testimony to their poor body condition and how difficult arousal is for kangaroo rats under these circumstances (Yousef and Dill 1971).

Torpor patterns (frequency, depth, duration) appear to vary substantially between individual kangaroo rats. The frequency histogram of hourly T_b of one kangaroo rat was bimodal with a relatively large range of values whereas the frequency histogram of the second kangaroo rat was unimodal but negatively skewed and had a relatively small range of values. Because hourly T_b measurements were unlikely to be independent of one another for statistical comparisons, I calculated the minimum sample size for which the observed differences in the frequency distributions would be significant. In all cases, minimum sample sizes that would be required were so small that the observed differences in frequency distribution would have been significant even if I had been limited to one measurement of T_b per 18 h or more. It would be feasible for a kangaroo rat to reach a substantially different T_b every 18 h. Therefore I am confident that my statistical comparisons of the frequency distributions of T_b between individuals and seasons (early versus late winter) are robust to the assumption of independence of observations and reflect clear differences between thermoregulation of individuals and seasons. Despite the substantial differences between the thermoregulation profiles of the two individual kangaroo rats, I cannot extrapolate from these individuals' patterns to make inferences about sexual differences or annual variation in torpor patterns of the population. These data represent two different winters with differing ambient conditions, so I cannot infer the relative contribution of annual differences in weather conditions, nor variation between individuals or sexes. However, in combination with my results from radio telemetry studies (Gummer 1997, Chapter 4), it is apparent that individuals do show substantial variation in the intensities and characteristics of torpor: some individuals use deep torpor and others do not, even during the same seasons, in close proximity, and presumably with comparable availability of food aboveground and other

microsite characteristics (Chapter 4). Some radio-collared individuals did not show any evidence of torpor whatsoever (Gummer 1997, Chapter 4) but the ability to discriminate shallow torpor episodes from externally attached radio-collars is low. This is where internal measurements of T_b by implanted dataloggers excel: the shallow torpor of the second kangaroo rat may not have been detected by monitoring T_{sk} . In other species, such as bats, there can be temperature differences of up to 3.3 °C between T_b and T_{sk} (Barclay et al. 1996). It is plausible that many kangaroo rats use relatively shallow torpor while many other individuals use torpor of significantly greater depth and duration.

There are many factors that may potentially contribute to the large amount of variation in torpor patterns among individual kangaroo rats. Torpor capabilities may be affected by quantity or composition of food caches, body size or condition, gender, age, or ambient conditions. One would need to recover winter thermoregulation profiles from a much larger number of kangaroo rats to test for effects of these factors on variation in torpor use within the population. These types of comparisons may be feasible now that the use of torpor has been confirmed and a field technique has been established (Chapter 5). Such efforts would be especially likely to be productive in years or areas with relatively high over-winter survival, or if individual kangaroo rats could be marked with both implanted dataloggers and miniature radio transmitters, simultaneously, to enhance recovery of dataloggers from kangaroo rats that disperse to new sites, die in their underground burrows, or are eaten by predators.

I found that kangaroo rats were more likely to use daily torpor on days with cold minimum temperatures and deep snow. Similarly, torpor depth and duration were related to air temperature and snow conditions. These findings are not surprising given that

kangaroo rats would presumably experience difficulty finding food in extreme cold and deep/continuous snow cover (Reynolds 1958, Kenagy 1973, O'Farrell 1974).

Communally nesting white-footed mice (*Peromyscus leucopus*) have also been found to show patterns of daily torpor that are related to ambient weather conditions (Lynch et al. 1978). However, to my knowledge, kangaroo rats are one of few species that exhibits extended, seasonal dormancy with torpor patterns that vary on a daily basis according to ambient weather conditions. The fact that kangaroo rat torpor patterns vary on a daily basis under natural, seasonal conditions is intrinsically consistent with the typical life history of desert species: they need to opportunistically capitalize on favourable conditions whenever they occur, which tends to be unpredictable in desert environments (Kenagy and Bartholomew 1985, Brown and Harney 1993). Although this concept is more conventionally applied with respect to the scarcity of food resources in xeric environments except after unpredictable precipitation events, it also appears to apply to the northernmost kangaroo rats whose aboveground activity and foraging opportunities are instead constrained by extremely cold air temperatures and an abundance of winter precipitation.

The focus of my thermoregulation studies was on the winter season. However, it is possible that kangaroo rats may use torpor occasionally during other times of the year. Torpor and aestivation (torpor at relatively high temperatures; Hudson 1978, Lehmer et al. 2003) might be predicted to occur in kangaroo rats when or where the availability of new food resources becomes limited by inclement weather conditions, including periods of severe aridity. However, the advantage of conservation of metabolic resources by torpor also imposes at least one important cost: torpid animals cannot respond quickly to external stimuli (French 1993). Torpid kangaroo rats would be much more susceptible to

predators that can enter or excavate their burrow systems, such as snakes or mammalian carnivores, particularly during the summer when these predators typically show high levels of abundance and activity in kangaroo rat habitats. Similarly, the underground food caches of torpid kangaroo rats would be more vulnerable to theft by conspecifics or other granivores, especially during summer when the levels of abundance and activity of other granivores is high. Kangaroo rats are renowned for their aggressive territorial defence behaviour to safeguard food caches (Eisenberg 1963). For these reasons, torpor in kangaroo rats may be expected to occur predominantly during those periods when ambient conditions not only increase the need for metabolic conservation but also reduce the risks of underground predation or theft of food resources from burrows.

Now that it is clear that northern Ord's kangaroo rats use daily torpor during winter, it will be critical to apply comparable field techniques to other conspecifics and congeners, particularly populations that occupy high altitudes and more moderate latitudes. Do Ord's kangaroo rats in Montana, Wyoming, Washington, or Oregon use torpor to any extent? Do Merriam's or panamint kangaroo rats use torpor at some of the highest elevations that they inhabit in Nevada and California? It would be worthwhile to conduct systematic studies of kangaroo rats at regular intervals along climatic gradients within the overall geographic distribution of the genus (Appendix B). Given that I have established a field technique for effectively monitoring thermoregulation of free-living kangaroo rats, and so much else of the physiological ecology of kangaroo rats is already well documented (French 1993), I suggest that kangaroo rats may prove to be a productive study system for further examination of geographic variation in thermoregulation and energetics. Furthermore, the technique of implanting miniature temperature dataloggers in small endotherms to assess thermoregulation of free-living

animals (Mzilikazi et al. 2002, Lehmer et al. 2003, Mzilikazi and Lovegrove 2004) should also be applied to other taxa, especially northernmost populations of species that may have been mistakenly presumed not to use torpor.

The wide diversity of species that is now known to use torpor under natural conditions provides increasing evidence that torpor is plesiomorphic. The northernmost population of Ord's kangaroo rats may be the only population, or one of few populations, of kangaroo rats that express torpor successfully in nature. Long-term geographic isolation at the northernmost periphery of the species geographic range (Kenny 1989, Gummer 1995) may have promoted recurrence of expression of existing genetic traits that facilitate torpor.

The case of winter thermoregulation and torpor in kangaroo rats illustrates that new approaches for descriptive and explorative research have an important role in physiological ecology. Herein, I have documented a field technique that can be broadly applied systematically across species geographic ranges to document thermoregulation under natural conditions and I have established that peripheral populations at high latitude or altitude are efficient, logical starting points for field studies of thermoregulation and torpor capabilities. Ultimately such studies will contribute to understanding of macroecological patterns between climate and energetics, biological diversity, and potential effects of changes in climate or food availability on populations and distributions of species.

Conclusion

I found that northern Ord's kangaroo rats successfully use daily torpor as an over-winter strategy, particularly during periods of cold and snow. I reported descriptive

and exploratory analyses of patterns of torpor among northern kangaroo rats. At least for the northernmost population, torpor appears to be well developed and ecologically relevant. Systematic field studies of thermoregulation across the geographic range of the species and genus are needed to evaluate if torpor is endemic to the northernmost population or if torpor is more widespread and had been overlooked due to a lack of field studies of thermoregulation. Peripheral populations at climate extremes provide valuable opportunities for field evaluations of thermoregulation and torpor in general, and the approach of implanting small dataloggers in free-living animals should facilitate field studies of thermoregulation that will increase knowledge of variation in torpor. My findings, on a genus whose physiological ecology was previously considered well documented, underscore the continuing importance of effective field studies in physiological ecology.

CHAPTER 4. RELATIONSHIPS BETWEEN TORPOR, SURVIVAL, AND BODY CONDITION OF NORTHERN ORD'S KANGAROO RATS

Introduction

Kangaroo rats (*Dipodomys*) are nocturnal, granivorous rodents that have well known physiological and behavioural adaptations to hot, arid environments of western North America (French 1993, Tracy and Walsberg 2002). Two species (*D. merriami* and *D. ordii*) have much wider geographic and climatic distributions than the majority of species in the genus, with Ord's kangaroo rats (*D. ordii*) occurring across the widest range of latitude (20 to 51 °N; Schmidly et al. 1993, Chapter 1). The northernmost population of Ord's kangaroo rats presumably experiences relatively harsh winter conditions and appears to exhibit low over-winter survival rates (Gummer 1997) compared to more southern congeners and desert rodents in general (Kenagy and Bartholomew 1985, Waser and Jones 1991, Brown and Harney 1993, Jones 1993). Predators are arguably unlikely to be a major cause of winter mortality in the northern population because kangaroo rats remain underground in their burrows during cold periods of continuous snow cover (Reynolds 1958, O'Farrell 1974, Kenny 1989, Gummer 1997), thereby reducing aboveground exposure time to many predator species (e.g., *Canis latrans*, *Bubo virginianus*). Furthermore, many other predator species are absent during winter due to seasonal migration habits (e.g., *Athene cunicularia*) or are inactive due to seasonal dormancy (e.g., *Crotalus viridis*). Hence, over-winter mortality

is most likely caused by starvation and hypothermia in underground burrows during periods of cold ambient temperatures (T_a) and continuous snow cover that increase resource requirements at the same time as preventing efficient foraging for new food resources.

Northern Ord's kangaroo rats are also the only population of the genus that is known to use torpor under natural winter conditions (Chapter 3). Torpor confers substantial conservation of metabolic resources (Vogt and Lynch 1982, Prothero and Jurgens 1986, Wang and Wolowyk 1988), thereby increasing the amount of time that kangaroo rats should be able to survive on a given amount of stored food. Some kangaroo rats appear to use relatively deep torpor (minimum $T_b < 15$ °C) whereas other individuals exhibit much more shallow deviations from normothermy (e.g., minimum $T_b = 27.5$ °C; Chapter 3). However, quantification of the extent to which torpor use varies among kangaroo rats and seasons has not been possible due to a small effective sample size of individuals and seasons (Gummer 1997, Chapter 3).

While torpor clearly imposes substantial metabolic advantage compared to normothermy (Vogt and Lynch 1982, Prothero and Jurgens 1986, Wang and Wolowyk 1988), importantly there are also potential costs of torpor. Kangaroo rats have small body mass (*ca.* 70 g; Gummer 1997) and very low amounts of body fat (Schreiber and Johnson 1975). Arousal from low T_b is the most energetically costly part of torpor and accordingly, starving kangaroo rats (e.g., *D. merriami*) in captivity apparently die from an inability to arouse from torpor (Dawson 1955, Carpenter 1966, Yousef and Dill 1971, Breyen et al. 1973, MacMillen 1983). Hence there is a potential survival cost to northern kangaroo rats that enter torpor without sufficient energy resources to maintain minimum T_b and successfully arouse. Another potential cost of torpor is increased risk of

predation: although predators are not likely to contribute to a large proportion of winter mortality among northern kangaroo rats, mild weather that reduces snow cover may increase the risk of predation from some resident predator species (e.g., *Canis latrans*, *Mustela nivalis*) by making kangaroo rat burrows more conspicuous and accessible. Torpid animals cannot respond to threat of predation by initiating appropriate anti-predator behaviour because they are much less aware of their environment and less mobile than euthermic animals (Carpenter 1966, French 1993). The need to remain vigilant may deter some kangaroo rats from using torpor in their underground nests. Additionally, kangaroo rats are highly territorial and strenuously defend their territories and food caches from theft by conspecifics and other granivores (Bartholomew and Caswell 1951, Eisenberg 1963, Behrends et al. 1986, Jones 1993). Torpid animals may inadvertently suffer from theft of stored food resources by other animals that remain active (French 1993). Torpor is also likely to compromise spermatogenesis for males (Meistrich et al. 1973, Barnes et al. 1986, Barnes et al. 1987, Kurta et al. 1988, Michener 1992) and embryo development for pregnant females (Racey 1973, Racey and Swift 1981, Kurta et al. 1987, Audet and Fenton 1988, Grinevitch et al. 1995). The reproductive season of northern kangaroo rats is typically spring through summer (Kenny 1989, Gummer 1997). Reproduction may constrain use of torpor during that time and the potential for earlier or later reproduction in some years may also affect expression of torpor at other times of year. Clearly there are many theoretical benefits and costs of torpor that are likely to contribute to expression of torpor.

It is not presently known to what extent and under what circumstances torpor is used among different individuals and varying seasons, and how torpor ultimately relates to survival and body condition of northern kangaroo rats. Laboratory experiments with

captive kangaroo rats collected from more southern localities have demonstrated that torpor can be induced by extreme starvation at cold T_a to a near death state (Dawson 1955, Carpenter 1966, Yousef and Dill 1971, Breyen et al. 1973, MacMillen 1983). These studies have shown that kangaroo rats that are starved and exposed to cold T_a promptly lose considerable amounts of body mass before entering torpor and once they begin using torpor they die within four to six days (Carpenter 1966). Even when arousal from torpor is assisted by passive heating, the majority of kangaroo rats cannot successfully arouse from torpor (Yousef and Dill 1971). Hence torpor has generally been considered an unsuccessful strategy for kangaroo rats and the ecological relevance of torpor was essentially dismissed (MacMillen 1983, French 1993). However, I demonstrated that northern kangaroo rats are capable of expressing (at least) 26 consecutive daily torpor bouts under natural, free-living conditions and manage to survive winter having maintained body mass (Chapter 3). Additional research is needed to evaluate the extent of torpor use among individuals, seasonal patterns of torpor use, and to document if the majority of kangaroo rats that use torpor actually survive the winter or have better body condition than kangaroo rats that do not use torpor. Northern kangaroo rats provide a good opportunity for investigating the relative prevalence and effectiveness of different thermoregulatory strategies for over-winter survival. Details describing over-winter survival and body condition of kangaroo rats that use torpor are also needed to further clarify the differences between the torpor expression of northern kangaroo rats and torpor as it is expressed by starving, dying congeners from more southern populations (Dawson 1955, Carpenter 1966, Yousef and Dill 1971, Breyen et al. 1973, MacMillen 1983).

The purpose of my study was to examine patterns of torpor use and evaluate whether survival rates and body condition differ among kangaroo rats that use torpor and those that do not. There are at least three conceivable roles of torpor in the northern population of kangaroo rats. Given my previous findings (Gummer 1997, Chapter 3), it is unlikely that northern kangaroo rats adopt torpor only when they are dying from starvation at cold T_a . However, if this is the case, then individuals that use torpor during winter would be less likely to survive and would be in poorer body condition than kangaroo rats that do not use torpor. Alternatively, kangaroo rats may minimize torpor, entering torpor only when body condition, underground food caches, or microclimate necessitate additional measures for conservation of metabolic resources. This appears to be the pattern of torpor use exhibited by captive kangaroo mice (*Microdipodops*; Brown and Bartholomew 1969) and pocket mice (*Chaetodipus* and *Perognathus*; Tucker 1966, Wolff and Bateman 1978). If this is the case for northern kangaroo rats, then kangaroo rats that use torpor would be expected to survive the duration of winter and maintain body condition at least as well as individuals that do not use torpor, with potentially higher over-winter survival during particularly cold or long winters. Lastly, given that torpor can facilitate conservation of substantial metabolic resources (Vogt and Lynch 1982, Prothero and Jurgins 1986, Wang and Wolowyk 1988), some individual kangaroo rats may maximize use of torpor to conserve food resources and thereby effectively extend the duration of the period that they can survive potentially unfavourable conditions. In this case, use of torpor would be expected to enhance survival and body condition beyond that of animals that do not use torpor. Based on previous studies of northern kangaroo rats (Gummer 1997, Chapter 3) and other heteromyid rodents (Brown and Bartholomew 1969, Tucker 1966, Wolff and Bateman 1978), I predicted that

kangaroo rats that use torpor should survive and maintain body condition at least as well as kangaroo rats that do not use torpor.

Methods

I studied Ord's kangaroo rats in the Middle Sand Hills (50° 35' N 110° 23' W) of southeastern Alberta, Canada, which represents the extreme northernmost periphery of the species geographic range (Schmidly et al. 1993, Chapter 1). To facilitate simultaneous monitoring of a relatively large number of kangaroo rats, I identified two study sites that appeared to have high numbers of kangaroo rats living in close proximity to one another. Both study sites were representative of prairie habitats that northern kangaroo rats typically occupy: steep, sparsely vegetated, sandy slopes of the South Saskatchewan River valley. One study site (*ca.* 60 ha) was subjected to anthropogenic disturbance associated with gas pipeline construction during my study whereas the other study site (*ca.* 116 ha) was an undisturbed, natural site in Canadian Forces Base Suffield National Wildlife Area.

Beginning in July 2001, I surveyed the study sites on foot on alternating nights, searching open sandy habitats with bright handheld spotlights. Any kangaroo rats that were observed were pursued on foot and caught by hand (Gummer 1997, Gummer et al. 1997). I recorded the geographic coordinates (± 10 m Universal Transverse Mercator zone 12, North American Datum 1983) of capture locations using a handheld global positioning system (Garmin 12XL, Olathe, Kansas). Each kangaroo rat was marked with one uniquely numbered metal eartag (Monel 1005-1, National Band and Tag Co., Newport, Kentucky) and a microchip (12 mm Fecava, Avid Canada, Calgary, Alberta) for reliable identification (Williams et al. 1997). The microchip was injected

subcutaneously between the scapulae using a sterile 12 gauge needle. I determined the sex of each kangaroo rat and I measured body mass (± 1 g) using a spring-scale (Pesola, Switzerland). I attached miniature temperature-sensitive radio transmitters (1.5 g MD-2CT, 164 – 166 MHz, Holohil Systems, Carp, Ontario) to kangaroo rats as radio-collars (Gummer 1997, Harker et al. 1999) while the animals were anesthetized with IsoFlo (isoflurane) inhalant administered from a custom vaporizer. The collars were attached by threading the whip antenna through plastic tubing that was cut to match the approximate circumference of the animal's neck, slipped over the animal's head and tightened to an appropriate fit. A small metal crimp was used to pinch the antenna, thereby securing the collar. Each radio-collared kangaroo rat was released at the exact location from which it was captured earlier that night. The radio-collars had an approximate battery life of 60 to 70 d.

I monitored radio-collared kangaroo rats using a handheld radio telemetry receiver (R-1000, Communications Specialists, Orange, California) equipped with a yagi antenna (Telonics, Mesa, Arizona). On average I located kangaroo rats in their daytime nests every 1 to 2 d to determine their location, T_{sk} , and fate. I estimated T_{sk} (± 0.25 °C) by first measuring the pulse rate of the radio signal using a stop-clock (± 0.1 s) and then calculating the temperature of the transmitter according to quadratic equations that represented the relationship between temperature and pulse rate for each transmitter. I considered T_{sk} to be reasonably representative of T_b given that the thermistor of the transmitter was located on the inside of the collar, adjacent to major blood flow to and from the brain of the study animal. Furthermore, laboratory experiments with other species have shown externally attached, temperature-sensitive radio transmitters provide useful estimates (± 3.3 °C) of T_b across a range of T_a (Barclay et al. 1996). As radio

transmitter batteries began to fail in mid-autumn, I attempted to recapture each kangaroo rat and replace its collar with a new radio transmitter prior to the upcoming winter. I expected that the second batch of radio-collars would fail during mid-winter but I considered that this would provide an adequate monitoring period to assess which individuals were prone to torpor and their relative survival. As soon as I documented the first evidence of daily torpor in more than one individual, I began intensive hourly daytime telemetry monitoring of kangaroo rats at each study site on alternate days. I considered $T_{sk} < 30$ °C to represent daily torpor to exclude T_{sk} variation due to microclimate and euthermic activity levels (Michener 1992, Gummer 1997). According to my study of T_b in other kangaroo rats by implanted miniature dataloggers, some individuals frequently use very shallow torpor (Chapter 3). I may not have detected such shallow deviations from normothermy according to T_{sk} . Therefore, I acknowledge that individuals that were presumed not to have used torpor may in fact have used shallow torpor and simply did not express torpor to as great a depth as the other group of study animals.

I revisited the study sites to conduct live capture surveys on equal numbers of nights during autumn (October 2001), mid-winter (January 2002), and the subsequent spring (April 2002) to attempt to recapture individual kangaroo rats to confirm survival, assess body condition, and remove expired radio-collars.

To describe variation in torpor use I calculated the proportion of individuals that were observed to use torpor each day. For each kangaroo rat I determined the maximum known depth of torpor (minimum T_{sk}) and number of torpor bouts that were observed. I assigned individual kangaroo rats to one of two groups: those that exhibited torpor with

minimum $T_{sk} < 30$ °C and those that did not. Individuals that died before the period in which torpor was observed were not included in statistical analyses.

I evaluated survival during radio telemetry monitoring using the Kaplan–Meier product limit estimator (Kaplan and Meier 1958, Krebs 1989) with a staggered entry design (Pollock et al. 1989, Winterstein et al. 2001). Given a relatively small number of individuals that were monitored intensively during winter, I used a Fisher exact test to examine whether over-winter survival was independent of torpor use. To do so, I assumed that the probability of detecting survival of individual kangaroo rats was equal regardless of whether they used torpor during the preceding winter or not. For all subsequent statistical analyses I treated torpor status as a random independent variable because some individuals that I assigned to the non-torpor group could possibly have used torpor that I did not detect. All other factors were treated as fixed effects for Analyses of Variance (*ANOVA*). To examine whether pre-winter body condition was related to torpor use, I conducted a mixed model *ANOVA* to test for main effects of torpor, study site, sex, and age class on pre-winter (October) body mass. I also examined whether mid-winter and spring body condition differed among kangaroo rats that used torpor and those that did not by applying Analyses of Covariance to test for main effects of torpor and study site on change in body mass. In these analyses I included covariates to account for pre-winter body mass and the number of intervening days between observations of body mass. This approach assumed that rate of body mass change relative to pre-winter body mass was indicative of body condition. I did not report test statistics for variables that did not exert significant effects if they had been included in the model only in an attempt to control for factors that were not of primary interest.

I obtained daily weather data describing air temperature and snow depth for the nearest meteorological station (Medicine Hat Airport, 50° 35' N 110° 23' W; Environment Canada National Climate Archive 2004), which is located approximately 68 km south-southwest of my study area. To evaluate the relative severity of winter weather conditions during my study, I compared mean monthly air temperature and number of days with snow during my study period to the 95 % confidence intervals for 30-year climate normals (1971 to 2001; Environment Canada National Climate Archive 2004).

Results

I monitored thermoregulation and survival of 45 radio-collared kangaroo rats from 24 July 2001 to 16 January 2002 (177 d). There was no evidence of torpor use from 24 July to 24 October (Fig. 4.1) based on 1317 estimates of T_{sk} from 41 individuals during that period (range 4 to 91 estimates per individual). Survival declined during this time (Fig. 4.1), with known fates including four kangaroo rats that were eaten by prairie rattlesnakes (*Crotalus viridis*) and nine suspicious disappearances that I attributed to other unidentified predators.

From 24 October to 30 November, three kangaroo rats used shallow torpor on four different dates. During this period there was only one mortality (Fig. 4.1), a kangaroo rat had apparently been trampled by elk (*Cervus elaphus*). Radio-collars of three kangaroo rats also expired during this period but could not be replaced because the kangaroo rats were not recaptured until the subsequent spring. The first date that more than one individual was observed to enter torpor was 1 December, during which 4 of 28 kangaroo rats (14 %) were recorded in torpor (Fig. 4.1). From 1 December to 16 January

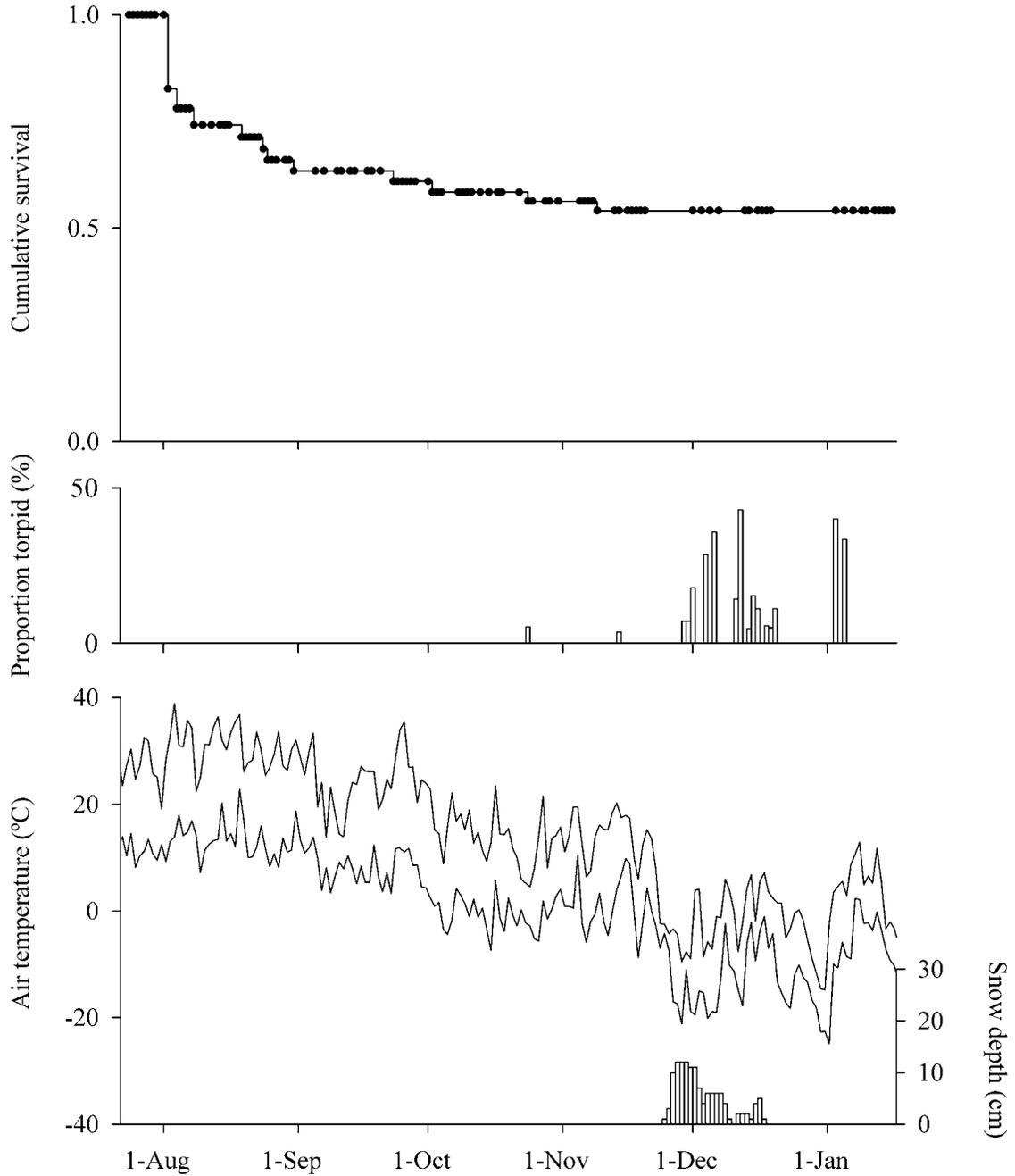


Figure 4.1 Cumulative survival of 45 radio-collared kangaroo rats from 24 July 2001 to 16 January 2002 (top graph), relative to the seasonal distribution of torpor use (middle graph) and daily weather conditions (bottom graph). Proportion torpid (middle graph) indicates the proportion of individuals that were monitored that exhibited torpor on a given date. The bottom graph shows daily maximum and minimum air temperature and vertical bars indicate daily snow depth (on the secondary ordinate), obtained from the Environment Canada National Climate Archive (2004).

I documented torpor use by 9 of 28 radio-collared kangaroo rats (32 %) with minimum T_{sk} ranging from 13.0 to 29.0 °C (Table 4.1). The proportion of individuals that used torpor on any given day during winter ranged from 0 to 43 % (Fig. 4.1). All of the mortalities of radio-collared kangaroo rats occurred prior to the winter torpor period (Fig. 4.1), thereby precluding statistical comparison of survival rates between kangaroo rats that used torpor and those that did not. However, survival rates of both groups were very high (100 %) and did not appear to differ during the winter torpor period. I also recaptured 25 of 28 radio-collared kangaroo rats (89 %) during the subsequent spring. There was not a significant difference in the spring recapture rates of kangaroo rats that used torpor and those that were not known to use torpor during the preceding winter (Fisher exact $P = 0.23$).

Pre-winter body mass did not differ among kangaroo rats that were known to use torpor and those that were not ($F_{[1,23]} = 1.772$, $P = 0.20$), although body mass varied significantly among the study sites ($F_{[1,23]} = 11.51$, $P = 0.003$), sexes ($F_{[1,23]} = 13.06$, $P = 0.001$), and ages ($F_{[1,23]} = 37.22$, $P < 0.001$). Eight of 13 kangaroo rats (62 %) that were weighed in both late autumn and mid-winter gained body mass during that period. Kangaroo rats that used torpor had significantly smaller mid-winter gains in body mass than kangaroo rats that did not use torpor (Fig. 4.2; $F_{[1,9]} = 8.245$, $P = 0.018$). Similarly, I found that spring body condition of kangaroo rats that used torpor was poorer than that of kangaroo rats that did not use torpor (Fig. 4.3; $F_{[1,12]} = 8.209$, $P = 0.014$).

My review of weather data and climate normals indicated that my radio telemetry study coincided with warm mean monthly air temperatures and very few days

Table 4.1 Details of winter thermoregulation and over-winter survival of 28 radio-collared kangaroo rats at the northernmost periphery of the species geographic range.

| Torpor status | Sex | Age | Number of days monitored ¹ | End date ² | Minimum T_{sk} (°C) | Torpor bouts ³ | Survived? ⁴ |
|---------------------------------------|--------|----------|---------------------------------------|-----------------------|-----------------------|---------------------------|------------------------|
| <i>Known to use torpor (n = 9)</i> | | | | | | | |
| | male | adult | 5 | 19-Dec | 27.25 | 2 | Yes |
| | male | adult | 7 | 7-Jan | 14.25 | 5 | Yes |
| | male | juvenile | 5 | 19-Dec | 13.00 | 2 | Yes |
| | female | adult | 4 | 12-Dec | 28.75 | 1 | Yes |
| | female | adult | 7 | 19-Dec | 22.50 | 6 | No |
| | female | adult | 9 | 20-Dec | 17.00 | 4 | Yes |
| | female | juvenile | 7 | 19-Dec | 14.50 | 3 | No |
| | female | juvenile | 7 | 19-Dec | 29.00 | 1 | Yes |
| | female | juvenile | 9 | 5-Jan | 21.50 | 1 | Yes |
| <i>No evidence of torpor (n = 19)</i> | | | | | | | |
| | male | adult | 7 | 19-Dec | 32.25 | 0 | Yes |
| | male | adult | 7 | 19-Dec | 31.25 | 0 | Yes |
| | male | adult | 9 | 20-Dec | 36.00 | 0 | Yes |
| | male | adult | 9 | 20-Dec | 34.75 | 0 | Yes |
| | male | adult | 13 | 10-Jan | 36.00 | 0 | Yes |
| | male | adult | 7 | 10-Jan | 37.00 | 0 | Yes |
| | male | juvenile | 5 | 13-Dec | 34.75 | 0 | No |
| | male | juvenile | 7 | 19-Dec | 32.00 | 0 | Yes |
| | male | juvenile | 9 | 20-Dec | 30.25 | 0 | Yes |
| | male | juvenile | 15 | 16-Jan | 32.00 | 0 | Yes |
| | female | adult | 2 | 1-Dec | 34.25 | 0 | Yes |
| | female | adult | 4 | 7-Dec | 30.00 | 0 | Yes |
| | female | adult | 6 | 18-Dec | 30.50 | 0 | Yes |
| | female | adult | 7 | 19-Dec | 35.00 | 0 | Yes |
| | female | adult | 9 | 20-Dec | 33.00 | 0 | Yes |
| | female | juvenile | 2 | 3-Dec | 35.25 | 0 | Yes |
| | female | juvenile | 5 | 7-Dec | 34.75 | 0 | Yes |
| | female | juvenile | 9 | 20-Dec | 30.00 | 0 | Yes |
| | female | juvenile | 9 | 20-Dec | 31.00 | 0 | Yes |

¹Number of winter dates for which the T_{sk} of the individual was estimated on an hourly basis

²Date of last T_{sk} monitoring due to expiry of radio transmitter batteries

³Number of known torpor bouts with $T_{sk} < 30$ °C

⁴Was the individual recaptured during the subsequent spring (April 2002)?

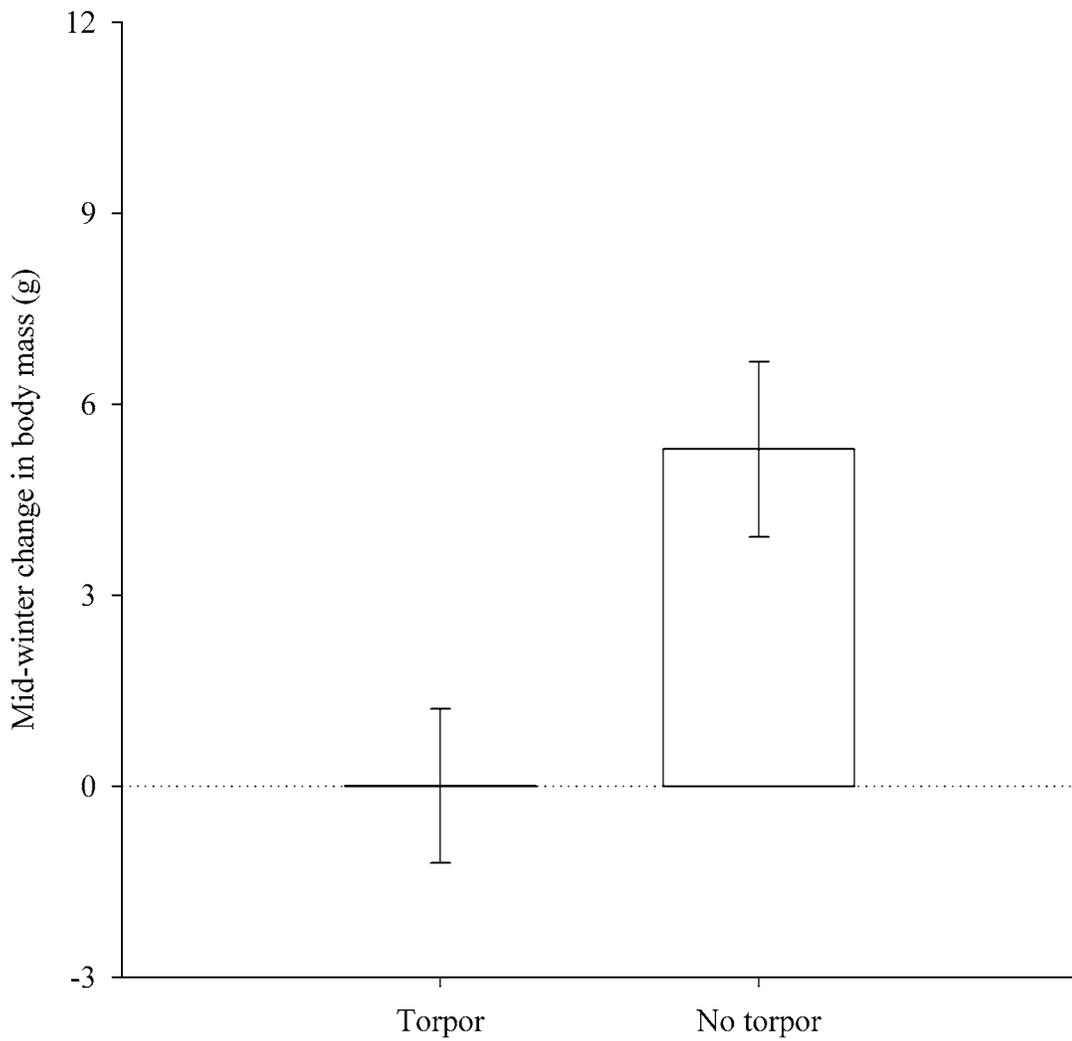


Figure 4.2 Mean (± 1 standard error) of mid-winter body condition (mid-winter mass minus preceding autumn mass) for northern Ord's kangaroo rats that used torpor during early winter ($n = 6$) and those that were not known to use torpor ($n = 7$).

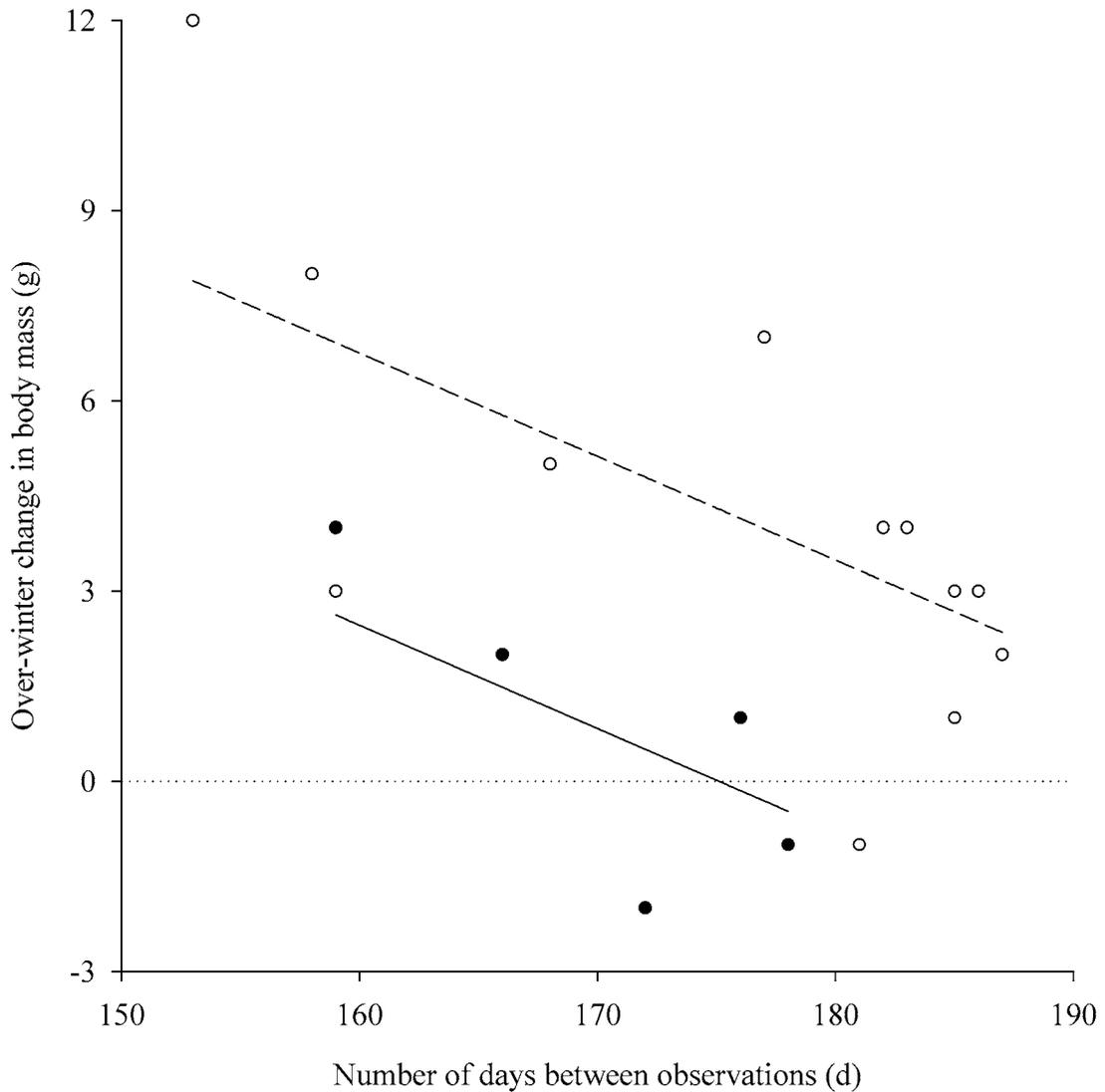


Figure 4.3 Spring body condition (spring mass minus preceding autumn mass) for northern Ord's kangaroo rats that used torpor during early winter ($n = 5$; black circles and solid line) and those that were not known to use torpor ($n = 12$; open circles and dashed line). Number of days between observations was a significant covariate ($F_{[1,12]} = 15.50, P = 0.002$).

with snow on the ground compared to 30-year climate normals (Fig. 4.4). However, I found the opposite trend during late winter and spring: beginning in March, mean monthly air temperature was considerably colder and there were more days with snow on the ground compared to 30-year climate normals (Fig. 4.4).

Discussion

I used radio telemetry to evaluate thermoregulation and survival of a relatively large number of kangaroo rats and I determined that 32 % of individuals that were monitored during the winter torpor period exhibited clear evidence of torpor. This proportion may have reflected the relatively mild weather conditions that presumably moderated weather constraints on foraging opportunities. The relatively low proportion of kangaroo rats that were observed to use torpor may in part have also been affected by the fact that radio telemetry monitoring was necessarily restricted to the first part of the winter due to battery limitations of the radio transmitters. Among those kangaroo rats that were not known to use torpor during early winter, some individuals may have used torpor later in winter. The only means of evaluating late winter torpor would have been intraperitoneal implantation of miniature temperature dataloggers (Chapter 3) or radio transmitters with larger batteries. I attempted implantation of miniature temperature dataloggers in other kangaroo rats at different study sites but the surgical protocol appeared problematic, resulting in a low number of kangaroo rats successfully being implanted with dataloggers (Chapter 5). Notably, two kangaroo rats from which I successfully recovered implanted dataloggers each appeared to exhibit similar patterns of thermoregulation during early and late winter in both years of study (Chapter 3). One of these individuals consistently used shallow torpor with $T_b \geq 27.5$ °C despite the

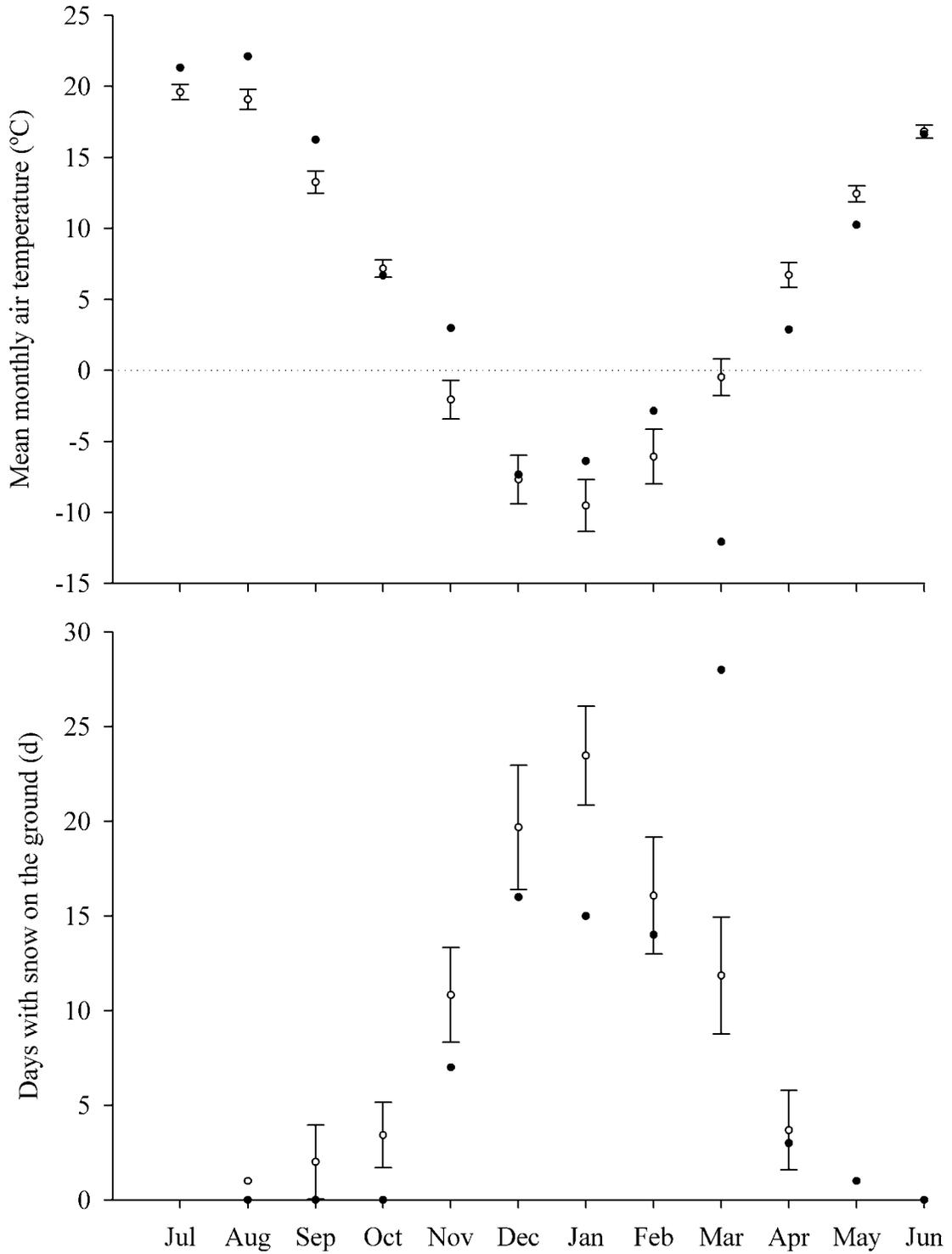


Figure 4.4 Mean monthly air temperature and number of days with snow on the ground during my study (July 2001 to April 2002; solid circles) and 30-year climate normals (mean \pm 95 % confidence intervals; open circles with error bars) for the nearest meteorological station to my study area (Medicine Hat Airport, Alberta; Environment Canada National Climate Archive 2004).

extreme cold T_a and deep snow during late winter (March 2002). The other implanted kangaroo rat used deep torpor in both early and late winter (Chapter 3). Hence there is anecdotal support that early winter observations may provide an accurate indication of whether or not an individual is likely to use torpor during late winter.

My study provides the first documentation of the temporal distribution of torpor in free-living kangaroo rats during summer and autumn. My results clearly demonstrate that kangaroo rats do not use torpor during summer or early autumn, which corresponds to the period of greatest mortalities from predation, relatively mild temperatures, and absence of snow. If expression of torpor was strictly dependent on T_a then I would have expected torpor to be used more frequently during autumn. From 29 September to 23 November, for example, daily minimum T_a was consistently < 5 °C yet shallow torpor was detected on only two occasions during this period (see Fig. 4.1). Kangaroo rats may remain euthermic to be vigilant for predators or granivores that might steal from their underground food caches (French 1993). The observation that the majority of mortalities appeared to be associated with predators suggests that there is significant risk of predation during the pre-winter period. Prairie rattlesnakes accounted for at least 27 % of mortalities of kangaroo rats during late summer and autumn, and are frequently observed using kangaroo rat burrows in the study area. There may be strong selective pressure for northern kangaroo rats to remain euthermic and alert during periods when snakes or other predators are active. My study cannot separate the effect of predation risk from potential simultaneous effects of risk of food theft, mild weather, or microclimate. However, I suggest that northern kangaroo rats may provide a useful study system for experimental studies of tradeoffs between energetics of torpor and the

risk of predation or food theft because quantification and exclusion of predators and other granivorous animals in the field are likely to be achievable.

Kangaroo rats that used torpor during winter survived as well as kangaroo rats that were not known to use torpor. I expected to document that a measurable proportion of study animals died in their underground burrows during early winter because I had previously observed low over-winter survival from mark-recapture methods and preliminary results from radio telemetry (Gummer 1997). My intention then was to determine whether survival was influenced by the use of torpor. The absence of early- to mid-winter mortalities of radio-collared kangaroo rats was presumably related to the relatively mild winter conditions that prevailed during my study, thereby providing continued foraging opportunities for kangaroo rats throughout the majority of the radio telemetry monitoring period. I also observed a relatively high recapture rate of kangaroo rats after the radio-collars expired, despite the extremely cold T_a and large number of days with snow that occurred in the interim (March 2002). While it is plausible that starvation and hypothermia are less common than previously assumed (Gummer 1997), my study occurred during an exceptional year: January 2002 was the first time in seven years that kangaroo rats were observed to be active aboveground between November and March (pers. obs.). In fact, I observed kangaroo rats copulating on warm, rainy nights during January 2002. This anecdotal observation suggests that the potential for reproduction at any time of year may further constrain torpor use. More importantly, the mild conditions that prevailed during my study provided an unexpected but valuable context for interpretation of torpor among northern kangaroo rats. Winter weather conditions appear to be sufficiently variable and unpredictable that torpor is not always

necessary. In fact, torpor may be avoided when moderate winter weather conditions allow for continued foraging aboveground.

My finding that kangaroo rats that used torpor survived as well as kangaroo rats that were not known to use torpor further distinguishes the torpor expressed by northern kangaroo rats from that which has been documented among starving, dying congeners from more southern localities (Dawson 1955, Carpenter 1963, Yousef and Dill 1971, Breyen et al. 1973, MacMillen 1983). The majority of northern kangaroo rats that I observed to use torpor survived, and even maintained body mass during the winter; however, contrary to my prediction they exhibited poorer mid-winter and spring body condition in comparison with kangaroo rats that did not use torpor. Apparently kangaroo rats that remained euthermic gained considerable body mass over the course of the winter by accomplishing more feeding from existing underground food caches or winter foraging opportunities. I could not quantify the status of kangaroo rats' underground food caches and therefore I could not discern whether some kangaroo rats did not use torpor specifically because of the high quantity or quality of their pre-existing food stores, or alternatively if they gradually improved their food stores and body condition as a result of remaining active for feeding and gathering new food. Regardless of the exact nature of the underlying, causal relationship, my findings suggest that energetic benefits of torpor may be outweighed by benefits of normothermy during periods with relatively moderate winter weather. Importantly, this interpretation does not necessitate the assumption that all kangaroo rats enter the torpor period with comparable food stores: even individuals with the largest food caches would be expected to use torpor if it enabled them to further conserve food caches and body condition, unless there are diminishing benefits of torpor due to other factors. The observation that kangaroo rats

that remain euthermic possess better mid-winter and spring body condition than kangaroo rats that use torpor suggests that the potential costs of torpor, such as risk of hypothermia, predation, food theft, or lost reproductive opportunities, exceed the metabolic advantages that would be conferred by adopting deep torpor. Kangaroo rats may use deep torpor only during those periods when it is necessitated due to limited availability of food resources, which is dictated not only by weather conditions but also by the status of accumulated underground food caches. Northern kangaroo rats may not enter torpor in response to cold winter weather, snow conditions, or harsh burrow microclimates *per se*, but instead may use these cues to gauge the adequacy of current food caches, foraging opportunities, and the relative urgency of using torpor to conserve metabolic resources. Captive kangaroo mice and pocket mice are known to match their use of torpor to the availability of food (Tucker 1966, Brown and Bartholomew 1969).

The observation that kangaroo rats that used torpor did not exhibit higher over-winter survival than individuals that remained euthermic does not negate the potential importance of torpor for northern kangaroo rats. Torpor is likely to be a critical strategy for over-winter survival of some individuals, and potentially for the majority of individuals in years when the duration and severity of winter weather are more extreme. Daily torpor can conserve up to 38 % of euthermic energetic expenditures of small mammals (Vogt and Lynch 1982). That is, a kangaroo rat that uses torpor with $T_b \leq 20$ °C for $12 \text{ h} \cdot \text{d}^{-1}$ could theoretically extend the period that it could survive on a finite amount of seeds by at least 38 % (assuming $Q_{10} = 2.5$; Prothero and Jurgens 1986). One relevant measure of winter severity, the cumulative number of days with snow on the ground (per year), is highly variable in my study area, ranging from 42 to 125 d over the last 30 years (mean \pm SD = 82 ± 24 d; Environment Canada National Climate Archive

2004). During years with particularly long periods of snow cover, even those kangaroo rats with the largest food caches at their disposal may need to use torpor to endure the duration of the winter.

Life history strategies of desert rodents are tied to unpredictable environmental conditions, as exemplified by the relationships between unpredictable precipitation events and timing of reproduction of heteromyids (Beatley 1969, Reichman and Van De Graaf 1975, Beatley 1976, Hoditschek and Best 1983, Best and Hoditschek 1986). For the northernmost population, the unpredictability of winter weather conditions is likely to be a major factor that contributes to variation in thermoregulatory patterns and over-winter survival. In some respects, for the northernmost population of kangaroo rats winter severity may be analogous to intermittent droughts experienced by more southern congeners. Desert rodents generally need to persist through long arid periods to facilitate reproduction during more favourable conditions (Stearns and Crandall 1981, Kenagy and Bartholomew 1985). Similarly, northern kangaroo rats need to persist through long periods of winter cold and snow to facilitate reproduction when aboveground conditions are more favourable.

It seems likely for a food-storing animal such as northern Ord's kangaroo rats, that torpor patterns are directly related to the size or quality of underground food caches and the prospect of continued foraging opportunities. However, it is also possible that some individuals may be genetically predisposed to entering torpor (Hudson 1978) and these two different physiological strategies may be maintained in the population due to variation in the relative success of each strategy depending on food availability. This idea was originally proposed by Hudson (1978), who suggested that for many species daily torpor is likely to be expressed by only a fraction of the population but that this

strategy remains in the population because in some years it is favoured by limitations on availability of food. Notably, based on his observations of relationships between torpor and food stores in other heteromyids, Hudson (1978) also correctly predicted that some species or populations of kangaroo rats might eventually be found to use torpor in nature. I cannot address whether genetic differences may account for variation in expression of torpor but it is clear that additional field experiments that quantify thermoregulation, food caches, predation risk, severity of winter, and genetic relationships, will be required to provide additional insights on expression of torpor among kangaroo rats.

Conclusion

Northern Ord's kangaroo rats are the only population of the genus *Dipodomys* that is known to use torpor under natural winter conditions but variation in torpor use and the relative effectiveness of torpor at facilitating over-winter survival was previously unknown. I found, during relatively mild winter conditions, that northern kangaroo rats that use torpor exhibit similarly high rates of over-winter survival as kangaroo rats that remain euthermic. In contrast kangaroo rats that use torpor exhibit poorer mid-winter and spring body condition than kangaroo rats that remain euthermic. My findings suggest that the energetic benefits of torpor may be outweighed by benefits of euthermy, because individuals that have sufficient food appear to avoid using torpor, thereby minimizing risks of torpor and simultaneously maintaining body condition better than kangaroo rats that use torpor. Clearly torpor use varies considerably among individuals and between years, but torpor confers substantial metabolic savings and thereby increases the period that an individual can survive on limited food resources. Hence it is

likely that torpor accounts for a greater proportion of over-winter survival during years with greater duration or severity of winter. Further studies of torpor in northern kangaroo rats could attempt to evaluate tradeoffs that contribute to torpor expression by measuring or manipulating food caches and risk of predation or food theft, simultaneous to quantifying thermoregulation, body condition, and winter severity.

CHAPTER 5. MONITORING THERMOREGULATION OF SMALL MAMMALS IN THE WILD

Introduction

Heterothermy may be more common and widespread among endotherms under natural conditions than previously recognized (Hudson 1978, Geiser et al. 2000). Improved understanding of heterothermy will require new studies conducted in the field, where physiological and behavioural patterns frequently differ in comparison to those of captive animals (Geiser et al. 2000). I implemented field methods to evaluate thermoregulation of black-tailed prairie dogs (*Cynomys ludovicianus*) and Ord's kangaroo rats (*Dipodomys ordii*) at the northernmost peripheries of the species ranges. I discovered seasonal hibernation and daily torpor in northern prairie dogs (Chapter 2) and kangaroo rats (Chapters 3 and 4), respectively, despite the general beliefs that have persisted for decades that these taxa do not hibernate or use torpor under natural conditions (Hamilton and Pfeiffer 1977, MacMillen 1983, Harlow and Menkins 1986, Bakko et al. 1988, French 1993, Harlow 1995, Hoogland 1995, Harlow 1997, Hoogland 1997, Harlow and Frank 2001, Lehmer and Van Horne 2001).

The use of hibernation and daily torpor by the northernmost prairie dogs and kangaroo rats may be endemic to those populations of the species; they likely experience more harsh winter conditions than southern conspecifics (Appendix B). Prairie dogs and kangaroo rats both appear to be well studied in terms of their physiology and ecology:

there are large numbers of published laboratory studies of captive animals and field studies of aboveground behaviour of these taxa (see French 1993, Hoogland 1995). The physiology and behaviour of the animals under these conditions have in turn contributed to many perspectives and comparative approaches in physiological and behavioural ecology (Hamilton and Pfeiffer 1977, Armitage 1981, Michener 1983, Michener 1984, MacMillen 1983, Harlow and Menkins 1986, French 1993, Harlow 1995, Hoogland 1995, Harlow 1997, Harlow and Frank 2001). However, review of the literature regarding these species and their congeners reveals that there have actually been few previous studies of thermoregulation or energetics of these taxa under natural field conditions. To my knowledge there have been three published field studies of thermoregulation (Bakko et al. 1988, Lehmer et al. 2001, Lehmer et al. 2003) in free-living black-tailed prairie dogs, all of which occurred in relatively close geographic proximity near the centre of the species geographic range. I am aware of no published field studies of thermoregulation of free-living kangaroo rats. Field studies are necessary to understand the significance of torpor to survival and fitness of free-living animals under natural conditions (Geiser et al. 2000) because laboratory experiments with captive animals can be confounded in unexpected ways. For example, the observation that synchrony of hibernation in alpine marmots (*Marmota marmota*) is compromised in captivity (Geiser et al. 2000) indicates that conditions of captivity may affect social hibernators differently than solitary hibernators. Hence laboratory studies of social black-tailed prairie dogs may not reflect the physiology and behaviour of the animals under more natural conditions. Similarly, the observation that starving, dying kangaroo rats that have been experimentally deafened enter torpor earlier and spend more time in torpor than those that have not been deafened (Carpenter 1966) suggests that auditory

disturbances in captivity may affect torpor use in these species, which are known to be particularly sensitive to low frequency auditory signals (Webster and Webster 1975). To clarify the extent to which animals use torpor in the wild and to test the general hypothesis that thermoregulation and energetics vary on a geographic basis will require additional field investigations of thermoregulation of prairie dogs, kangaroo rats, and other taxa across climatic gradients.

Thermoregulation of free-living animals is frequently studied by telemetric methods in the field (e.g., Wang 1979, Bakko et al. 1988, Michener 1992, Körtner and Geiser 2000, Zervanos and Salsbury 2003, Fletcher et al. 2004). Radio transmitters can be attached externally to small animals as a collar (Michener 1992, Gummer 1997, Chapter 4), backpack (Fletcher et al. 2004, Lane et al. 2004), or glued to the skin (Hamilton and Barclay 1994, Barclay et al. 1996, Tracy and Walsberg 2002), or they can be surgically implanted in the subcutaneous (Daly et al. 1992) or peritoneal cavity (Bakko et al. 1988, Van Vuren 1989, Zervanos and Salsbury 2003). Temperature sensitive radio transmitters use a thermistor that modulates the pulse interval of the transmitter predictably with changes in temperature, thereby allowing the observer to estimate the temperature of the transmitter according to known calibration curves. Physical size, mass, and antenna configuration of radio transmitters are major considerations for telemetric studies because they influence the strength of the radio signal, longevity of the battery, and potential effects of the transmitters on the study animal's behaviour, physiology, or ecology.

Recent technological advances in miniature dataloggers have facilitated a new approach for studying thermoregulation: implantation and recovery of small temperature recorders (*ca.* 3.3 g) in animals, a technique that is becoming more common in field

research (Nicol and Andersen 2000, Lehmer et al. 2001, Mzilikazi et al. 2002, Lehmer et al. 2003, Harlow et al. 2004, Mzilikazi and Lovegrove 2004, Taylor et al. 2004).

Dataloggers sample temperature at regular intervals, thereby providing a semi-continuous record of T_b and avoiding potential pitfalls of non-random temporal sampling of thermoregulation (Taylor et al. 2004). While small dataloggers could conceivably be attached externally, one of the main advantages of dataloggers is that they do not require a radio antenna and therefore they can be implanted within the bodies of small animals. Dataloggers themselves are also much less costly than radio transmitters and require no specialized telemetry receiving equipment. The main constraint of the datalogger technique is that it necessitates recapture and recovery of the datalogger from the animal, which can be unpredictable (e.g., Chapter 3). Surgical implantation also appears to be difficult but this is in part because detailed surgical procedures are rarely communicated in the literature. Therefore, the objectives of this paper are: (i) to provide details of my procedures for studying thermoregulation of prairie dogs and kangaroo rats; (ii) to document whether surgery or carrying the implanted datalogger appears to compromise body mass and survival of the animals; and (iii) to discuss tradeoffs between common field techniques for studying thermoregulation of free-living animals.

Methods

Animal captures

I live-trapped black-tailed prairie dogs at the northern periphery of the species geographic range during autumn (October and November) and spring (April and May) by setting wire mesh traps (50 x 15 x 15 cm, custom-built traps and model 202, Tomahawk Live Trap, Tomahawk, Wisconsin) baited with peanut butter and rolled oats.

I caught Ord's kangaroo rats at the northernmost periphery of the species geographic range during autumn (October and November) and spring (April) by "nightlighting", which involves driving a vehicle slowly ($< 30 \text{ km} \cdot \text{h}^{-1}$) with spotlights (10^6 candlepower; Brinkmann, Dallas, Texas) aimed at open sandy areas and edges of vegetation (Kaufman and Kaufman 1982, Gummer 1997, Gummer et al. 1997, Ralls and Eberhardt 1997). Kangaroo rats that were observed by nightlighting were pursued on foot and caught by hand (Gummer 1997, Gummer et al. 1997). I also conducted live-trapping in the vicinity of known kangaroo rat burrows using custom metal live-traps (Sherman-style) baited with rolled oats and equipped with terylene bedding material (Radvanyi 1964).

For both species, I recorded the geographic coordinates ($\pm 10 \text{ m}$ Universal Transverse Mercator zone 13U, North American Datum 1983) of capture locations using a handheld global positioning system (Garmin 12XL, Olathe, Kansas). Each animal was marked by subcutaneous injection of a microchip (12 mm Fecava, Avid Canada, Calgary, Alberta) using a sterile 12 gauge needle. Animals were placed in cloth bags and transported to a mobile surgery (van) or field station, where they were transferred to small animal cages for temporary holding prior to the surgical procedure.

Dataloggers

I used Tidbit dataloggers (StowAway Tidbit, Onset Computer, Bourne, Massachusetts; Lehmer et al. 2001, Lehmer et al. 2003) to measure T_b of prairie dogs. I acquired the dataloggers from the manufacturer as bare circuit boards ("unpotted") because I intended to coat the dataloggers with two layers of physiologically compatible wax (paraffin/elvax, Mini-mitter, Sun River, Oregon) and to minimize the overall mass

of the implant. Before coating the dataloggers with wax, I covered them with plastic heat-shrink tubing. The wax-coated Tidbit dataloggers measured 35 mm in diameter and 19 mm in depth, with a mass of 16 g (*ca.* 2 % of the mean body mass of prairie dogs). The battery life of these dataloggers is reportedly up to 5 yr and they can store 32,520 measurements in nonvolatile memory. Thus in the eventuality of a datalogger failure, previously recorded data would likely still be recoverable. The Tidbit dataloggers measure temperature with an accuracy of ± 0.4 °C from -5 to 44 °C and the accuracy of the real-time clock is ± 1 min per week. I programmed dataloggers to record T_b once every 30 min.

For the much smaller kangaroo rats, I used iButton dataloggers (DS1921, iButton ThermoChron, Dallas Semi-conductor, Dallas, Texas; Mzilikazi et al. 2002, Mzilikazi and Lovegrove 2004) to measure T_b . I coated the iButton dataloggers with one layer of physiologically compatible wax because they were already waterproof. The iButton dataloggers measured 16.3 mm in diameter, 5.9 mm in depth, and weighed 3.3 g (*ca.* 5 % of the mean body mass of kangaroo rats). They record up to 2048 consecutive time-stamped temperature measurements and record the cumulative total number of temperature measurements in frequency histograms with 2 °C classes. Temperature is measured with an accuracy of ± 1 °C from -20 to 70 °C and the accuracy of the real-time clock is ± 2 min per month from 0 to 45 °C. I programmed iButton dataloggers to record time-stamped T_b measurements once every hour over a period of 85 d. I programmed half of the dataloggers that I deployed to store time-stamped temperature readings during the first 85 d and the other half of the dataloggers to store time-stamped temperature readings during the most recent 85 d (*i.e.*, overwriting the oldest data with the most recent measurements), in anticipation that some of each type, representing early

and late winter thermoregulation, would be recovered. Regardless which 85 d for which the dataloggers stored time-stamped readings, they all recorded cumulative histograms of hourly temperature for the entire winter (November through April).

The wax-coated dataloggers could not be steam sterilized at high temperature (*ca.* 132 °C) because the wax would melt and the temperature dataloggers could fail. Therefore I had the wax-coated implants gas sterilized with ethylene oxide at a local dentistry clinic. I also needed to disinfect some dataloggers in the field, which I accomplished by immersing the dataloggers in Savlon (chlorhexidine gluconate) for 2 minutes, followed by a sterile saline rinse.

Anesthesia and surgical procedure

To ensure proper dosage of anesthesia and analgesia, I determined the body mass of each study animal (± 10 g for prairie dogs and ± 1 g for kangaroo rats) immediately before surgery by weighing it in a cloth bag using a spring-scale (Pesola, Switzerland). During autumn 1999 and spring 2000, I anesthetized prairie dogs by administering an intramuscular injection of Telazol ($10 \text{ mg} \cdot \text{kg}^{-1}$, tiletamine and zolazepam, Fort Dodge Laboratories, Fort Dodge, Iowa; Woodbury 1996) using a 0.30 ml syringe with a 29 gauge needle. Beginning in autumn 2000, I anesthetized all prairie dogs and kangaroo rats with IsoFlo (isoflurane, Abbott Laboratories, Saint-Laurent, Quebec) inhalant. I induced IsoFlo anesthesia by placing the animal in a plastic induction chamber and administering 3 to 4 % IsoFlo and $1 \text{ l} \cdot \text{min}^{-1}$ oxygen from a precision vaporizer. When the animal was anesthetized, I removed it from the induction chamber and I attached a small nose cone with a latex seal to administer 2 to 3 % IsoFlo with $0.5 \text{ l} \cdot \text{min}^{-1}$ oxygen from the vaporizer. For the remainder of the procedure, my assistant ensured that the

nose cone remained in position and monitored the animal's state of anesthesia and heart rate using a Littman small animal stethoscope. I administered an intramuscular injection of Anafen ($20 \text{ mg} \cdot \text{kg}^{-1}$, ketoprofen, Rhône Mérieux, Victoriaville, Quebec) to provide analgesia during surgery and recovery.

I placed the anesthetized animal in a dorsal recumbent position on a warm water bottle or electric heating blanket and I used animal clippers to shave a narrow line (1 x 7 cm for prairie dogs, 1 x 2 cm for kangaroo rats) along the ventral midline. To provide a local anesthetic at the incision site, I administered a subcutaneous injection of dilute (0.5 % for prairie dogs and 0.05 % for kangaroo rats) Marcaine ($3 \text{ mg} \cdot \text{kg}^{-1}$, bupivacaine hydrochloride, Sanofi Winthrop, New York, New York) along the midline of the abdomen. I scrubbed the abdomen with Betadine surgical scrub (7.5 % povidone-iodine, Purdue Frederick, Pickering, Ontario) followed by 70 % ethanol. I put on a surgical mask and sterile surgical gloves and then placed a sterile drape with a narrow opening (1 x 7 cm for prairie dogs, 1 x 2 cm for kangaroo rats) over the incision site.

I used a sterile no. 10 surgical blade to cut the skin and I used blunt, curved Metzenbaum dissecting scissors to cut along the *linea alba*. I used Adson delicate tissue forceps to manipulate tissue throughout the procedure. The incision was *ca.* 6 cm in length for prairie dogs and 1.5 cm in length for kangaroo rats. I placed a sterile, wax-coated datalogger in the abdominal cavity, or recovered and replaced the previous implant, and then I closed the *linea alba* using simple interrupted sutures *ca.* 0.4 mm apart, with 3-0 chromic gut using a taper point needle (1/2 circle) and Halsey needle holders. I closed the subcutis and skin separately with 4-0 clear absorbable monofilament suture and a cutting point needle (3/8 circle), using simple continuous sutures for the subcutis and intradermal interrupted sutures (buried knots) for the skin to

prevent the animals from chewing the sutures. I washed the incision site with sterile gauze and peroxide. I also applied a small amount of surgical adhesive (VetBond, 3M, London, Ontario) to further secure the incision.

After implantation of the datalogger and recovery from anesthesia, I kept the animals in small animal cages with bedding material and food (rolled oats) *ad libitum* for 2 to 4 h to monitor their recovery. When they appeared fully recovered, coordinated, and alert, I transported them back to the field site to be released at the exact locations from which they had been caught earlier that day (prairie dogs) or the preceding night (kangaroo rats). The implanted animals did not appear to have difficulty with locomotion or navigation: they all promptly maneuvered to burrows. I trapped the same sites during the subsequent spring (April and May) to attempt to recapture any implanted animals that had not dispersed or died during the intervening winter.

Statistical analyses

I evaluated whether prairie dogs that underwent the surgical procedure and carried datalogger implants exhibited poorer spring body mass than prairie dogs that were not implanted, by comparing masses using an Analysis of Variance (*ANOVA*) for a fixed effect of datalogger status (implanted or not) after accounting for variation due to sex and year (fixed effects). I used a two sample *t*-test to compare the spring body mass of each implanted kangaroo rat to the spring body masses of other kangaroo rats that were not implanted but belonged to the same sex and age class and were caught during the same period.

Results

I surgically implanted 20 prairie dogs with miniature temperature dataloggers, of which I recaptured and recovered dataloggers from 13 prairie dogs during the subsequent spring. In total, I conducted 33 surgeries on prairie dogs: on 18 occasions I anesthetized prairie dogs with Telazol and on 15 occasions I anesthetized prairie dogs with IsoFlo. There were no mortalities of prairie dogs during surgery or recovery under either anesthesia regime. Induction and recovery from anesthesia appeared to be more rapid with IsoFlo than with Telazol, and IsoFlo also provided opportunity for continuous fine-tuning of the depth of anesthesia during the procedure, which Telazol did not. Each surgery took *ca.* 45 to 60 min, including induction, preparation, surgery, and preliminary recovery from anesthesia. The surgical incisions of implanted prairie dogs appeared to heal well with no infections evident upon recapture during the subsequent spring. The wax-coated dataloggers were easily retrieved from the peritoneal cavities because they remained in a free-floating state in all but one prairie dog: the datalogger of one individual had become entangled in a thin layer of connective tissue that required disentanglement and sharp dissection to free the datalogger. Body mass of the implanted prairie dogs decreased over the course of the winter but their spring body mass did not differ significantly from that of other prairie dogs that were not implanted ($F_{[1,22]} = 0.48$, $P = 0.50$). Two implanted dataloggers failed over the course of the winter, apparently due to moisture penetrating through tiny openings in the wax coating. One of the two dataloggers that failed contained recoverable data in nonvolatile memory but the other did not.

Similarly, I attempted to surgically implant 16 kangaroo rats with miniature temperature dataloggers. The procedure took *ca.* 30 to 60 min, including induction,

preparation, surgery, and preliminary recovery. Unfortunately 7 of the first 13 attempts ended with mortalities during surgery or recovery. Kangaroo rats died during closure of the incision or shortly (up to 90 min) thereafter. I obtained additional veterinary assistance, advice, and necropsies, but could not confirm the cause of mortalities. To explore if mortalities were caused by a reaction to the anesthetic, I experimentally induced, maintained, and monitored one kangaroo rat under IsoFlo anesthesia for 53 min without conducting any invasive surgical procedure and no mortality occurred.

For the first 13 surgeries on kangaroo rats, I placed the animals on warm water bottles during surgery in an attempt to prevent hypothermia; however, I realized that the warm water bottles were relatively cool by the end of the procedure. Hence, the following year (autumn 2001) I used an electric heating blanket to better maintain T_b of the kangaroo rats for the duration of the surgical procedure. I observed no additional mortalities during subsequent surgeries.

I recovered one male out of five kangaroo rats that were successfully implanted in autumn 2000. It maintained its 67 g body mass from 4 November through 22 April (169 d) and did not exhibit significantly lower body mass than 15 other adult males caught during the same period ($t_{[14]} = -1.147$, $P = 0.135$). I also recovered one female of three kangaroo rats that were implanted during autumn 2001. It gained body mass from 65 to 69 g between 31 October and 15 April (166 d), at which time its body mass was not significantly lower than eight other adult females that were not implanted ($t_{[7]} = -1.102$, $P = 0.153$). Like those of the prairie dogs, the surgical incisions of the two implanted kangaroo rats that were recovered appeared to have healed well with no infections evident upon recapture during the subsequent spring. The wax-coated

dataloggers were easily retrieved because they remained in a free-floating state in the peritoneal cavities of kangaroo rats.

Discussion

I surgically implanted miniature temperature dataloggers in 20 black-tailed prairie dogs and 16 Ord's kangaroo rats to study thermoregulation at the northern peripheries of the species geographic ranges. I observed no mortalities of prairie dogs during surgery or recovery but a high proportion (54 %, n = 13) of kangaroo rats died during the procedure, until I improved methods for preventing hypothermia. I successfully recaptured and recovered temperature dataloggers from animals that survived over-winter under natural conditions. The thermoregulation profiles that I obtained illustrated that prairie dogs hibernated (Chapter 2) and kangaroo rats used daily torpor (Chapter 3) during the intervening winter. For both species, animals that underwent surgery and carried dataloggers had comparable spring body masses to other conspecifics that were caught during the same period, suggesting that the recaptured animals did not experience severe negative effects on body growth or maintenance. I suggest that surgical implantation and recovery of temperature dataloggers is a productive, straightforward technique that should be applied more broadly in field studies of thermoregulation. Details regarding the procedure that I used should be useful for future field studies of thermoregulation in prairie dogs, kangaroo rats, or other taxa among geographic areas of varying climatic conditions.

Prairie dogs appeared to fare well through surgeries under both Telazol and IsoFlo anesthesia. Telazol injection is more convenient and less costly than IsoFlo because it requires only a syringe and needle for equipment, in comparison to the

precision vaporizer, oxygen tank, regulator, and breathing circuit that are required for administering IsoFlo. However, given that surgery needed to be conducted in a warm, sheltered location to minimize risks of hypothermia, it was not difficult to have this additional equipment on hand. IsoFlo anesthesia was advantageous because it facilitated quick induction and recovery from anesthesia, and fine tuning of depth of anesthesia throughout the procedure. A similar conclusion was reached by Kreeger et al. (1998), in a comparison of ketamine-medetomidine (injection) and isoflurane for immobilization of black-footed ferrets (*Mustela nigripes*).

I found that two of the recovered dataloggers from prairie dogs had failed, apparently from encroachment of moisture through tiny perforations in the wax coating. Fortunately one of the dataloggers still contained useful, recoverable data in nonvolatile memory. In hindsight, I do not recommend obtaining unpotted, bare datalogger circuit boards from the datalogger manufacturer. Instead I recommend obtaining the dataloggers in the normal consumer state with a waterproof plastic case. These should still be coated with physiologically compatible wax to maintain the dataloggers in a free-floating, retrievable state, but if moisture encroaches through the wax coating then there would still be another barrier to protect the datalogger and minimize the chance of datalogger failure.

Given my findings and the recent studies of prairie dogs by Lehmer et al. (2001, 2003), implantation and recovery of miniature dataloggers has become a well-established method for documenting thermoregulation of prairie dogs. Application of this method more broadly in conspecifics in other geographic areas with varying climatic conditions (Appendix B) would assist in elucidation of intraspecific variation in thermoregulation and energetics. In addition, three species of congeners have been

presumed to hibernate (Tileston and Lechleitner 1966, Hoogland 1995) yet to my knowledge patterns of natural thermoregulation or energetics have never been examined in those species in the field. Ultimately inter- and intraspecific comparisons between thermoregulation and energetics of prairie dogs in different geographic areas are likely to offer considerable insights regarding expression of hibernation in these animals.

I found temperature dataloggers to be a much more useful approach for evaluation of thermoregulation in the field than telemetric methods that I attempted with northern black-tailed prairie dogs (unpubl. data). I previously deployed temperature sensitive radio-collars configured with a tuned loop antenna (15 g; 162 to 164 MHz model G3-BT, AVM Instrument, Colfax, California) on prairie dogs. The radio signals were completely attenuated by the soil when radio-collared prairie dogs retreated into their deep burrows, entirely precluding evaluation of underground thermoregulation patterns. I tried several telemetry receivers (TR-2, Telonics, Mesa, Arizona) and antennae (RA-2A, Telonics, and 3 element yagi, AVM Instrument), including insertion of a rigid coaxial cable equipped with an omni-directional antenna (Burrow Flexi-probe, AVM Instrument) up to 5 m into burrows but I could not detect any radio signals whatsoever—even when the radio-collared animal was detected aboveground and observed to enter the burrow just seconds previously. I noted that, upon lowering a radio-collar *ca.* 2 m into a prairie dog burrow, the radio signal became undetectable from aboveground. Therefore I could not effectively use temperature sensitive radio-collars to evaluate thermoregulation of black-tailed prairie dogs in their underground nests. Have previous researchers experienced this difficulty monitoring radio-collared prairie dogs, or other semi-fossorial species that utilize deep burrows in the soil? I am aware of only one previous study that reported using radio-collars in prairie dogs (Garrett and Franklin

1988) but they did not indicate whether or not they were able to receive radio signals when the prairie dogs retreated to their underground nests. Curiously, Bakko et al. (1988) implanted radio transmitters in the peritoneal cavities of free-living prairie dogs and acquired radio signals from the prairie dogs in their underground nests throughout the year. The discrepancy between my experience and the study of Bakko et al. (1988) presumably relates to potential differences in burrow depths, soil composition, radio transmitter signal strength, or transmitter antenna configuration. However, regardless of the underlying cause of the discrepancy, I found that implantation and recovery of temperature dataloggers proved to be a much more feasible means of studying thermoregulation of northern prairie dogs compared to radio telemetry efforts.

In contrast to the prairie dogs, it was evident that kangaroo rats experienced considerable difficulty with surgeries given the high level of mortality during the first 13 surgeries. The observation that no additional mortalities occurred during surgery once I began placing the animals on an electric heating blanket is suggestive that maintaining warm T_b during surgery is particularly critical for these small animals. Their small body size, and the concomitant high surface area: volume ratio, compared to prairie dogs should cause them to lose heat more rapidly, especially when the peritoneal cavity is opened. I did not initially use an electric heating blanket as part of my protocol because I had been advised not to do so by veterinary practitioners that reportedly observed other animals that were accidentally burned by electric heating devices. Hence I caution that an electric heating blanket should only be used during surgery if the temperature can be monitored by an assistant throughout the procedure. Given that an assistant is generally required to monitor anesthesia of the study animals, this additional task should be feasible and is likely to be worthwhile because it should favour successful implantation,

release, and ultimately recovery of larger numbers of small mammals with intraperitoneal temperature dataloggers.

I recommend the method of implanting and recovering temperature dataloggers as a useful alternative to telemetric methods for evaluating thermoregulation of small mammals under natural conditions. Dataloggers are relatively inexpensive in comparison with radio telemetry equipment, yet dataloggers also have the inherent benefit of sampling T_b at regular intervals for acquisition of semi-continuous thermoregulation profiles of study animals (Taylor et al. 2004, Chapters 2 and 3). The datalogger approach necessitates recovery of implanted animals and therefore this technique is only likely to be efficient in animals that can be recaptured relatively predictably (i.e., non-migratory species). In some cases, recovery of dataloggers could potentially be enhanced by simultaneously implanting a radio transmitter in each animal. Ultimately a combination of the datalogger technique and other methods such as telemetry and stable isotope techniques for estimating field metabolic rate (*FMR*; Mullen 1971, Nagy and Gruchacz 1994, Schmid and Speakman 2000) are likely to provide important details of heterothermy of free-living endotherms. However, for broad-scale investigation of natural thermoregulation and energetics across climatic gradients, the datalogger approach appears to be a feasible, efficient, and economical field method that can likely be applied to any small mammal that can accommodate at least a 3.3 g intraperitoneal implant. Over time, even smaller temperature dataloggers are likely to become available for such applications.

CHAPTER 6. SYNTHESIS

Major findings

I studied thermoregulation of black-tailed prairie dogs (*Cynomys ludovicianus*) and Ord's kangaroo rats (*Dipodomys ordii*) at the extreme northernmost peripheries of the species geographic ranges where they experience particularly harsh winter conditions relative to the majority of conspecifics and congeners (Appendix B). I found that northern prairie dogs hibernate (Chapter 2) and kangaroo rats use daily torpor (Chapters 3 and 4) during winter, although there is no evidence that the species use these heterothermic strategies in more southern localities (see MacMillen 1983, French 1993, Hoogland 1995, Lehmer and Van Horne 2001). Northern prairie dogs and kangaroo rats spend a considerable proportion of the winter in torpor: prairie dogs hibernate for up to $95 \text{ d} \cdot \text{yr}^{-1}$ and kangaroo rats enter daily torpor on up to $67 \text{ d} \cdot \text{yr}^{-1}$. For both species, I documented patterns of torpor, such as depth, duration, and seasonal trends, that conform to those of typical endothermic heterotherms (French 1986, Geiser and Ruf 1995, Geiser 2004). I observed that the probability of torpor use was highest during winter periods of cold ambient temperatures and deep snow. Given that prairie dogs and kangaroo rats had never been studied under as harsh, natural winter conditions as they experience at the northernmost peripheries of the species ranges, it was premature for previous authors to generalize that the species do not hibernate or use daily torpor under natural conditions. My findings provide unprecedented evidence that patterns of endothermic heterothermy vary intraspecifically on a geographic basis in association

with climatic gradients. Importantly, the capability of torpor has not previously been regarded as varying between populations of a species. Additional systematic field studies of thermoregulation across geographic ranges will be required to determine if endothermic heterothermy tends to vary predictably across geographic ranges in a manner analogous to well known biogeographical patterns in body size and allometry (Mayr 1956, Mayr 1963, Endler 1977, Freckleton et al. 2003, Meiri and Dayan 2003).

Implications and future directions

The discoveries that northern black-tailed prairie dogs and Ord's kangaroo rats are seasonal and daily heterotherms, respectively, complement the mounting evidence that suggests torpor is plesiomorphic (Malan 1996, Geiser 1998, Lovegrove et al. 1999, Grigg and Beard 2000). These two additional species that are now known to use torpor under natural conditions add a new subgenus (*Cynomys*) and genus (*Dipodomys*) to the already broad diversity of taxa that use hibernation and daily torpor (Geiser and Ruf 1995). Traditionally torpor was regarded as a specialized, derived adaptation (Wang and Wolowyk 1988); however, torpor is presumably a complex trait that necessitates interactions among large numbers of genes, the sum of which is extremely unlikely to have evolved repeatedly as independent secondary adaptations among a wide diversity of taxa. Notably the majority of closely related species and ancestors of prairie dogs and kangaroo rats are considered to hibernate (MacMillen 1983, French 1993, Goodwin 1995, Harlow and Frank 2001, Lehmer et al. 2003), again underscoring that torpor is more likely to occur from plesiomorphic characters than to arise repeatedly as analogous, apomorphic traits. The theory that endothermic heterothermy is ancestral will be even further strengthened if systematic field studies of thermoregulation yield more

evidence of geographic variation in endothermic heterothermy in additional taxa. Certain populations of species that occupy regions with relatively cold, long winters or scarcity of food, appear to be the most likely populations to express torpor. This concept also highlights the opportunity to capitalize on climatological and biogeographical information (e.g., Appendix B) to prioritize study populations for investigations of thermoregulation and energetic patterns—a novel approach for improving knowledge of torpor and the plesiomorphic nature of heterothermy in mammals.

Consideration of endothermic heterothermy as plesiomorphic implies that the complex genetic traits that are required for torpor are shared by a wide diversity of animals. Yet the observation that northern prairie dogs and kangaroo rats both appear to be geographically isolated from more southern conspecifics (Gummer 1995, 1997, 1999) suggests that genetic differences between populations may contribute to variation in torpor expression. An effective means of evaluating the prospective roles of genetic and environmental variation on expression of torpor would be to experimentally translocate animals among sites of varying climatic conditions. If prairie dogs or kangaroo rats that are translocated from relatively mild regions to more harsh climates eventually acclimatize and exhibit comparable torpor as animals from harsh climates, then it would be apparent that geographic variation in torpor expression is primarily a phenotypic response to environmental conditions. Alternatively, if animals translocated from mild regions to more harsh climates do not exhibit similar torpor patterns as animals from harsh climates, then it would appear that genetic differences between the populations account for differential expression of torpor. Given that the northernmost prairie dogs and kangaroo rats appear to be geographically isolated in regions that impose relatively harsh winter climate compared to southern conspecifics (Appendix B), and exhibit

torpor patterns that are fundamentally different than the thermoregulatory patterns expressed by southern conspecifics (Chapters 2 to 4), I suggest that genetic drift may have facilitated recurrence of expression of plesiomorphic heterothermy in the northernmost populations of both prairie dogs and kangaroo rats. If true, such a pattern may also be characteristic of other endotherms given that species typically become more sparsely distributed, with adjacent populations apparently exchanging fewer immigrants/emigrants, towards the peripheries of species geographic ranges (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000).

Experimental translocations have high potential to provide insights on the relative influence of genetic and environmental factors on expression of hibernation and daily torpor. However, translocation of animals over long distances for release into free-ranging conditions may not be feasible, due to ecological risks such as disease transmission (e.g., sylvatic plague, *Yersinia pestis*; Biggins and Kosoy 2001) or potential for hybridization of species, subspecies, or potentially distinct populations (Hughes et al. 1997, Ceballos and Ehrlich 2002). Yet smaller scale translocations across abrupt climatic gradients may be feasible through coordination with conservation programmes (e.g., Robinette et al. 1995, Truett et al. 2001, Roe and Roe 2003). Alternatively animals could be translocated to outdoor enclosures for studies under semi-natural conditions. Laboratory studies of captive animals under more controlled conditions may be instructive if they elicit differing torpor patterns in animals from different source populations; however, laboratory approaches may be confounded if the effects of captivity vary among different source populations that have different (natural) thermoregulation patterns.

Clarification of the extent and underlying basis of geographic variation in thermoregulation and energetic patterns of endotherms will require additional systematic studies of a diversity of taxa. Fortunately, recent advances in miniature temperature datalogger technology have facilitated implantation and recovery of small (*ca.* 3.3 g) temperature recorders in small animals (Lehmer et al. 2001, Mzilikazi et al. 2002, Lehmer et al. 2003, Mzilikazi and Lovegrove 2004, Taylor et al. 2004). For researchers to implement comparable, effective field studies of thermoregulation, necessitates that details of the field technique are articulated. Therefore I reported specific details of my field procedures for capture, anesthesia, implantation and recovery of temperature dataloggers in prairie dogs and kangaroo rats (Chapter 5). This information should facilitate efficient, broad-scale studies of thermoregulation of free-living small mammals. Yet, I acknowledge that additional field methods will be useful for finer-scale studies regarding complexities of torpor expression and tradeoffs between the metabolic advantages and costs of torpor. Relationships between torpor use, survival, and body condition of radio-collared kangaroo rats strongly influenced my perspective on torpor in these animals by illustrating that (at least) during some years, or for some individual animals, the metabolic advantages of deep torpor do not necessarily outweigh the cumulative benefits of euthermia if sufficient food resources are available (Chapter 4). The combination of implanted dataloggers and telemetric methods may also be useful to enhance recovery rates of animals that are implanted with dataloggers (e.g., Taylor et al. 2004) in translocation experiments or systematic investigations of thermoregulation. Similarly these field methods could potentially be combined with stable isotope techniques (Nagy and Gruchacz 1994, Speakman 2000) or direct measurements of oxygen consumption in nest boxes (e.g., Schmid 1996) to estimate field metabolic rates

(FMR; Speakman 2000) that correspond to particular periods of heterothermy that are simultaneously recorded by implanted dataloggers. Experimental manipulation of food availability, predation risk, and density of intra- and interspecific competitors, are likely to be productive for examination of tradeoffs regarding torpor use by northern prairie dogs and kangaroo rats. Notably experiments of these kinds, such as food supplementation, exclusions of selected predators, reintroductions of specialized predators (e.g., black-footed ferrets, *Mustela nigripes*), and translocations of animals are likely to be feasible given their potential simultaneous value for ongoing conservation programmes. Furthermore, elucidation of the underlying basis and distinctness of thermoregulation and energetic patterns of the northernmost populations of prairie dogs and kangaroo rats will provide valuable context regarding the relative importance of peripheral populations for conservation of biological diversity (Appendix A). Variation in torpor capabilities may represent an important, but previously unrecognized component of population diversity (Hughes et al. 1997, Ceballos and Ehrlich 2002) that may influence the responses of populations to future changes in climate, food availability, or other anthropogenic factors that affect energetic constraints.

Intraspecific variation in torpor patterns of endotherms also provides unprecedented opportunities for comparative investigations of the underlying physiological and genetic basis of torpor expression. Many authors have compared torpor patterns among different species in attempts to determine and explain apparent fundamental differences in torpor capabilities (e.g., Harlow and Menkins 1986, Harlow 1995, Harlow 1997, Harlow and Frank 2001). While comparative interspecific approaches have an important role in documentation and elucidation of physiological and evolutionary patterns and processes, intraspecific comparisons should be more likely

to effectively control for a greater proportion of variation in aspects of the species' biology that could complicate or confound interspecific analyses. For example, torpor patterns of various taxa are affected differently by conditions of captivity (Geiser et al. 2000) and therefore comparisons of captive animals in laboratory experiments may be unlikely to discern relevant differences in physiology. Hence new intraspecific comparisons among populations of prairie dogs, kangaroo rats, and other taxa that exhibit fundamentally different torpor patterns should be more likely to reveal underlying physiological and genetic differences between animals that express torpor and those that do not.

Similarly, interspecific comparisons of behaviour and life history, including circannual patterns such as hibernation, frequently provide a basis for theories regarding behavioural and evolutionary ecology. For example, comparative studies of behaviour and life history of sciurids (Armitage 1981, Michener 1983, Michener 1984) have noted that the highest levels of sociality generally correspond to those species in which sex and age classes are simultaneously active: animals that interact for the largest proportion of time appear to be the most likely to develop relatively complex social relationships. Previous observations that black-tailed prairie dogs exhibit a high level of sociality, do not hibernate, and do not exhibit sex or age differences in circannual activity patterns, have significantly contributed to the interspecific trends that underlay these theoretical perspectives (Armitage 1981, Michener 1983, Michener 1984). My finding that northern black-tailed prairie dogs hibernate for a large proportion of the year does not necessarily deviate from the previously observed trends, because northern prairie dogs may continue to foster relationships throughout the hibernation season through synchrony of hibernation and social interactions during arousal (euthermic) periods. I did not observe

any tendencies for sex differences in hibernation patterns (Chapter 2) and unfortunately I could not accurately assess age classes of the implanted prairie dogs from which I recovered thermoregulation data. Additional field work will need to be conducted to determine conclusively whether there are sex and age differences in circannual thermoregulation and activity patterns of prairie dogs.

Notably, kangaroo rats also exhibit interspecific differences in behaviour and sociality that are loosely correlated with some life history traits (Jones 1993). The potential for some species or populations to exhibit different circannual activity patterns associated with winter conditions and use of torpor was not previously recognized, since the genus was not considered to use torpor in nature (MacMillen 1983, French 1993). If the seasonal timing of immergence into torpor is found to be variable among individuals, sexes, or age classes, of either species, then intraspecific comparisons may provide a particularly useful framework for examining tradeoffs regarding the relative timing of immergence into torpor. Potential intraspecific variation in torpor patterns, timing of associated circannual rhythms, and concomitant levels of sociality, across geographic ranges may facilitate opportunities for new intraspecific analyses that were not previously recognized as feasible. In addition, the observation of geographic variation of torpor patterns also suggests that previous assumptions about the behaviour and circannual activities of other taxa may require validation by new field studies in additional geographic areas. General interspecific patterns regarding hibernation and sociality may need to be revisited, with specific consideration of the potential for intraspecific, geographic variation in torpor patterns and the current lack of field studies of winter physiology and behaviour in many species. Theoretical perspectives may need

to be refined or perhaps new questions can be addressed, now that hibernation patterns are known to vary intraspecifically on a geographic basis.

Black-tailed prairie dogs and Ord's kangaroo rats are both likely to be good study systems for additional systematic investigation of geographic variation in thermoregulation and energetics. Each species has a relatively broad distribution in terms of latitudinal extent and climatic conditions (Appendix B). I established patterns of thermoregulation of the northernmost populations (Chapters 2 to 4) and I provided details of field procedures for effective documentation of thermoregulation (Chapter 5). Given the current paucity of field studies of thermoregulation and energetics, any field investigation of torpor in prairie dogs or kangaroo rats in any locality would undoubtedly facilitate valuable intraspecific comparisons. However, I suggest that studies of black-tailed prairie dogs and Ord's kangaroo rats that inhabit the next most extreme climatic conditions would be the most informative. Studies of the nearest conspecifics to the south and at relatively high elevations (e.g., Montana, South Dakota, Wyoming, Nevada), as well as the southern extremes of the species ranges (e.g., Mexico, Texas) are the most likely to clarify the full range of variation in natural torpor patterns of the species. Given the vastly different body size, life history, behaviour, phylogeny, and heterothermic patterns of prairie dogs and kangaroo rats, these taxa provide a good test of the generality of the hypothesis of geographic variation in torpor patterns and yet each study system is likely to provide different insights on torpor expression, as was the case in my studies.

Cumulatively, my findings underscore the vital importance of not extrapolating or generalizing beyond the range of conditions in which animals have been studied to date. Black-tailed prairie dogs and Ord's kangaroo rats are not the only species that are

likely to exhibit varying torpor expression among geographic areas. Torpor may have been overlooked in many species simply due to a lack of effective field studies of thermoregulation of animals under the most relevant conditions. The tendency of authors to presume that the characteristics of certain populations are adequately representative of the species is analogous to a Type II error in statistical analyses, where the probability of failing to reject a null hypothesis when the alternative hypothesis is true, is high given small sample size (Sokal and Rolff 1995, Zar 1999). That is, it is premature to generalize the physiological ecology of a species until it has been studied effectively throughout the entire range of conditions to which it is adapted. Therefore, there is an important continuing role of descriptive, explorative research in physiological ecology. Fortunately biogeographical and macroecological patterns and perspectives can be used to streamline field efforts and identify relevant study populations for particular research questions regarding patterns of thermoregulation and energetics.

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APPENDIX A. IMPORTANCE OF PERIPHERAL POPULATIONS

Abstract

Peripheral populations occur near the geographic range limits of species. Peripheral populations are often characterized by lower densities, are distributed among more heterogeneous habitats, and have reduced connectivity as compared to populations in more central areas of species ranges. As a result, peripheral populations generally have not been considered to warrant substantial and costly conservation programmes. However, recent analyses have suggested that species tend to persist more often near the periphery of species ranges than expected. I reviewed broad-scale patterns of distribution and abundance of species and the apparent persistence of peripheral populations. I suggest that disproportionate persistence near the peripheries has not been adequately demonstrated because of too liberal definitions of the peripheries. I provide a general model of peripherality that incorporates both: (i) proximity to range limits; and (ii) separation from central populations. There are many biological reasons to expect peripheral populations to contribute disproportionately more to species persistence. I propose that persistence of peripheral populations should be expected due to both population diversity and geographic segregation from spatially autocorrelated perturbations. Broad-scale conservation measures with particular emphasis on peripheral populations should maximize the likelihood that at least one population of a species will persist through periods of environmental change. Hence, peripheral populations likely have a more important role for biodiversity conservation than previously articulated.

Introduction

The periphery, or range limit, of the geographic distribution of a species occurs where population density declines to zero (Brown 1984). It is the boundary where the sum of immigration and births declines below the sum of emigration and deaths (Gaston 1990). Diverse abiotic and biotic factors contribute to the delineation of species range limits (Andrewartha and Birch 1954, Ehrlich 1961, MacArthur 1972, Krebs 1978, Strong 1979, Brown and Gibson 1983, Strong et al. 1984, Terborgh 1985, Davis 1986, Connor and Bowers 1987, Root 1988a, Root 1988b). Populations near the periphery occupy environments that present extreme values of the variables that govern whether the species can maintain a viable population or not, hence determining the location of the range limit.

Populations that occur near the periphery (henceforth peripheral populations) are typically expected to occupy less favorable habitats and exhibit lower and more variable population densities as compared to more central populations (Grinnell 1922, Andrewartha and Birch 1954, Udvardy 1969, Rapoport 1982, Hengeveld and Haeck 1982, Brown and Gibson 1983, Brown 1984, Gaston 1990, Hengeveld 1990, Maurer 1994, Lawton 1995, Brown et al. 1995, Hochberg and Ives 1999). Peripheral populations also tend to be distributed among more fragmented habitats and are less likely to receive immigrants from neighboring populations than are more central populations (Lomolino and Channell 1995, Lesica and Allendorf 1995, Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b).

For any population, the probability of extinction should be correlated with its population size and variability, and inversely correlated with density and immigration rate (MacArthur and Wilson 1967, Goel and Richter-Dyn 1974, Brown and Kodric-

Brown 1977, Pimm et al. 1988, Tracy and George 1992). These well established demographic patterns suggest that peripheral populations should be more prone to local extinctions than central populations; as species decline, geographic ranges should be expected to contract away from the peripheries. As a result, conservation measures have been presumed to be less effective in the peripheries (Griffith et al. 1989, Wolf et al. 1996). Conservation biologists tend to downplay peripheral populations and try to avoid peripheral populations when planning conservation strategies and allocating resources for endangered species (Griffith et al. 1989, Pearl 1992, Wolf et al. 1996, Araújo and Williams 2001, Rodrigues and Gaston 2002).

In contrast, recent analyses of species range collapses suggested that peripheral populations may often serve as the last remaining strongholds for species (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b). For example, the black-footed ferret (*Mustela nigripes*) of North America was presumed to be extinct for over a decade until one small and isolated population was discovered in 1981 at the western periphery of the species historical range (Anderson et al. 1986, Forrest et al. 1988), thereby providing a source of animals for captive breeding and subsequent reintroduction programmes (Biggins et al. 1999). For hundreds of diverse taxa for which historical and extant or final distribution maps were available, extant areas and final sites tended to occur in the peripheries of historical ranges more often than expected at random (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b; see also Brooks 2000). This biogeographical pattern was met with some reservation (e.g., Wolf et al. 1996) because it is counterintuitive to the expectation that peripheral populations should be more prone to extinctions than more central populations. It also

appears to be contradictory to the observed general successes of translocations of birds and mammals for conservation purposes (Griffith et al. 1989, Pearl 1992, Wolf et al. 1996, Lomolino and Channell 1998).

Channell and Lomolino (2000a, 2000b) contended that the observed propensity for species geographic ranges to collapse towards the peripheries differs from the pattern that would be expected according to demographic processes. Instead, they considered this pattern to be indicative of the contagion-like spread of extrinsic forces of extinction, most often anthropogenic disturbances, prompting their statement that “the geography of recent extinctions is largely the geography of humanity” (Channell and Lomolino 2000a:85). They suggested that populations that persist the longest should be those that are last affected by the extrinsic forces of extinction, such as sites near the peripheries of species ranges or in isolated, insular habitats (Channell and Lomolino 2000a). Channell and Lomolino (2000a) concluded that this pattern of persistence near the peripheries illustrates that peripheral populations may in fact have a valuable role for conservation of endangered species and biological diversity.

Clearly there is conflicting evidence as to the relative importance of peripheral populations. Therefore, the purpose of my paper is to review large-scale patterns of distribution and abundance of species and the apparent persistence of peripheral populations. I propose that the demographic and contagion hypotheses are not “different and competing paradigms within conservation biology” (Channell and Lomolino 2000b:170) because they are not necessarily mutually exclusive. A more dynamic hypothesis based on demographic processes should also consider that centres of high abundance (Sagarin and Gaines 2002), also known as “hot spots” (Brown et al. 1995), are not fixed in space. Rather, they could presumably migrate through time as conditions

change (e.g., anthropogenic habitat loss and fragmentation, or climate change)—a notion which has not yet been acknowledged with respect to geographic range collapses. Moreover, a combination of demographic and contagion-like processes should together contribute to persistence of species in the peripheries, because vulnerability of populations to extrinsic factors should often be correlated with demographic considerations such as the relative connectedness of populations. Lastly, population diversity (Hughes et al. 1997, Myers 1997, Ceballos and Ehrlich 2002, Luck et al. 2003) should be high in the peripheries of geographic ranges, which should also contribute to persistence of some peripheral populations (Lesica and Allendorf 1995, Lomolino and Channell 1995) but has been overlooked by recent evaluations and interpretations regarding patterns of collapses of geographic ranges (Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b).

Where possible, I quantitatively investigated various general patterns and models of peripherality using data describing the geographic distributions of 21 extant species of kangaroo rats (Heteromyidae: *Dipodomys*). By referring to this particular group of desert mammals I was able to maintain: (i) phylogenetic control—the species are closely related and should be approximately equally independent of each other, compared to an otherwise mixed group of species of more varying degrees of phylogenetic relatedness (Gaston et al. 1997); (ii) biogeographic control—the species are found in the same general biogeographic region, similar habitats, and are subject to similar environmental considerations; and (iii) geographic control—they are distributed over a relatively small extent of southwestern North America (Fig. A.1), thereby minimizing potentially confounding effects of different geographic map projections on distance and area calculations.

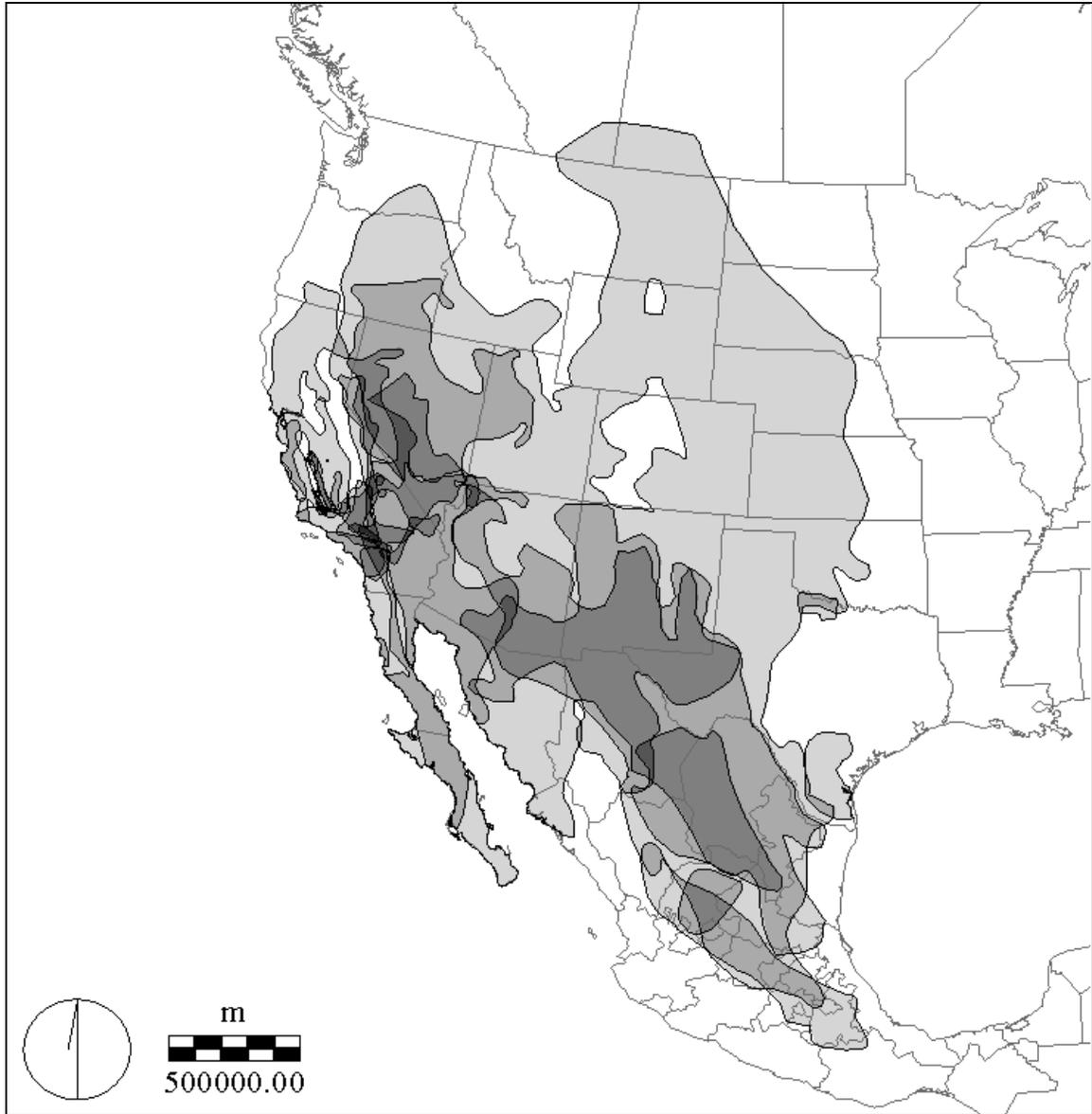


Figure A.1 The geographic distribution of kangaroo rats (Heteromyidae: *Dipodomys*) in southwestern North America (after Hall 1981). The grey tones represent incremental numbers of sympatric congeners (range = 1 to 6) whereas the black outlines represent the edges of each species range.

General patterns of distribution and abundance

Macroecology is founded on the assumption that large-scale patterns of distribution and abundance should provide insights into underlying ecological processes (Brown 1995, Blackburn and Gaston 2002, Nee 2002). General patterns of distribution and abundance may provide evidence regarding the susceptibility of species and populations to declines, collapses of geographic ranges, and the likelihood of persistence of peripheral populations.

Distribution of geographic range size

Ecologists have long recognized one such interspecific pattern: the relative abundance of geographic ranges of different sizes (Rapoport 1982, Brown 1984, Cody 1986, McAllister et al. 1986, Rabinowitz et al. 1986, Brown and Kurzius 1987, Schoener 1987, Gaston 1990). The frequency distribution of range sizes is highly skewed, with most species having small ranges and relatively few having large ranges (Brown 1984, Gaston 1990). As a result, a lognormal distribution often provides a good fit (Rapoport 1982, Gaston 1990). For example, the total area of the geographic ranges of kangaroo rats varies from approximately 170 to 3,420,000 km² and the frequency distribution is highly skewed, with the majority of species having small ranges and few having large ranges (Figs. A.1 and A.2, Table A.1). This pattern of range sizes has implications regarding the vulnerability of species to declines and collapses of geographic ranges (Purvis et al. 2000). Given that the majority of species have relatively small distributions, they are presumably more susceptible to extinction or range collapses from small-scale or regional perturbations than are the relatively few species that have larger geographic ranges.

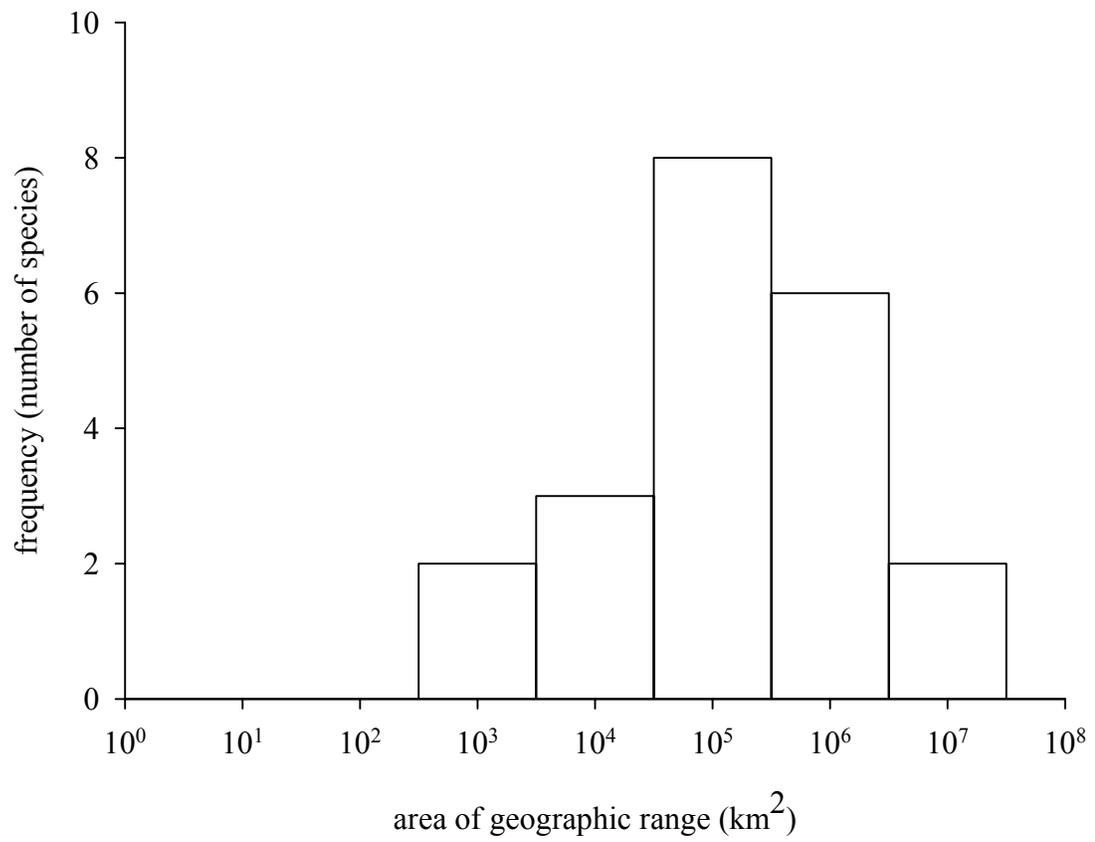


Figure A.2 The frequency distribution of geographic range sizes of 21 species of kangaroo rats plotted on a logarithmic scale (abscissa).

Table A.1 Geographic range metrics of 21 extant species of kangaroo rats (Heteromyidae: *Dipodomys*).

| Scientific name | Total area (km ²) | Periphery (km ²)* | Periphery (%)* | Max D_E (km) | Median D_E (km) |
|-------------------------|-------------------------------|-------------------------------|----------------|----------------|-------------------|
| <i>Dipodomys agilis</i> | 59633 | 45738 | 77 | 79 | 23 |
| <i>D. californicus</i> | 86171 | 63290 | 73 | 88 | 26 |
| <i>D. compactus</i> | 48819 | 31816 | 65 | 73 | 27 |
| <i>D. deserti</i> | 307679 | 241429 | 78 | 147 | 36 |
| <i>D. elator</i> | 12044 | 7562 | 63 | 40 | 15 |
| <i>D. gravipes</i> | 2221 | 1722 | 78 | 14 | 5 |
| <i>D. heermanni</i> | 70228 | 57004 | 81 | 71 | 17 |
| <i>D. ingens</i> | 6709 | 5504 | 82 | 16 | 4 |
| <i>D. insularis</i> | 169 | 118 | 70 | 5 | 2 |
| <i>D. margaritae</i> | 238 | 155 | 65 | 4 | 2 |
| <i>D. merriami</i> | 1415532 | 1070855 | 76 | 260 | 68 |
| <i>D. microps</i> | 392284 | 306002 | 78 | 205 | 53 |
| <i>D. nelsoni</i> | 192697 | 140480 | 73 | 177 | 54 |
| <i>D. nitratoides</i> | 11291 | 7752 | 69 | 15 | 5 |
| <i>D. ordii</i> | 3419620 | 2697854 | 79 | 445 | 125 |
| <i>D. panamintinus</i> | 60985 | 46301 | 76 | 49 | 15 |
| <i>D. phillipsii</i> | 176838 | 113840 | 64 | 96 | 36 |
| <i>D. simulans</i> | 113531 | 80872 | 71 | 60 | 20 |
| <i>D. spectabilis</i> | 523859 | 416154 | 79 | 176 | 48 |
| <i>D. stephensi</i> | 8409 | 5914 | 70 | 43 | 14 |
| <i>D. venustus</i> | 16363 | 13780 | 84 | 37 | 10 |
| Mean | 329777 | 254959 | 74 | 100 | 29 |

*According to the half edge-distance model (Channell and Lomolino 2000a)

Relationship between range size and abundance

In general, species that have relatively small geographic ranges also tend to be least abundant (Hengeveld and Haeck 1982, Bock and Ricklefs 1983, Brown 1984, Lacy and Bock 1986, Brown and Maurer 1987, Gaston 1988a, Gaston 1996, Blackburn et al. 1997, Gaston et al. 1997). Of course, species with restricted distributions should be expected to have smaller overall population sizes than species that have more widely distributed geographic ranges, but restricted species also tend to have lower abundances even at local scales (Hanski 1982, Brown 1984, Gaston 1996, Blackburn et al. 1997, Gaston et al. 1997, Gaston 1998, Johnson 1998). Among closely related species, those species that are specialized to capitalize on specific resources are less likely to expand their geographic ranges by attaining large population sizes, as compared to more generalist species (Brown 1984). Similarly, species that have narrow tolerances of environmental conditions should be less likely to expand their ranges by attaining large population sizes than more tolerant species. Species that have both small geographic ranges and relatively low abundance should be particularly susceptible to declines, range contractions, and extinction (Gaston 1998, Johnson 1998, Purvis et al. 2000).

Unfortunately, another contributing factor towards the apparent trend of a positive relationship between geographic range size and local abundance is that rare species are less likely to be detected and are therefore more likely to be assigned smaller geographic ranges simply as an artifact of sampling bias (Brown 1984, Gaston 1990, Gaston et al. 1997). In other words, “the greater the average abundance of a species, the more likely it would be to appear in samples and the greater would be its apparent range” (Brown 1984:264). This sampling bias surely contributes to the positive correlation between range size and abundance. However, the relative contribution of

sampling bias to the overall pattern of distribution and abundance has not been adequately quantified (Gaston et al. 1997). Brown (1984) considered that the bias in detection probabilities is not sufficient to explain the substantial increases in geographic range sizes that are observed to be associated with increases in local abundance. In addition, Brown (1984) stated that in many cases the boundaries of geographic ranges were known to be real, rather than inferred from the same datasets as local abundance. Similarly, Gaston et al. (1997) reviewed theories surrounding the relationship between local abundance and overall geographic range sizes and concluded that sampling bias alone cannot account entirely for the positive relationship between abundance and distribution. There are insufficient published estimates of local abundance (e.g., Brown and Harney 1993) to explore whether this general trend applies among kangaroo rats.

The apparent relationship between local abundance and overall size of geographic distributions appears to be different for ancient species than for more recent species (Johnson 1998). Johnson (1998) showed that, among Australian marsupial mammals there is a weak, positive correlation between local abundance and overall size of geographic ranges. However, when he partitioned ancient and recent species into separate groups he found that the positive relationship for recent species improved, whereas the relationship among ancient species became a significant negative correlation (Johnson 1998). The relative age of species, as evidenced by the number of extant species remaining in phylogenetic groups, illustrated that the combination of low abundance and narrow distribution makes species especially prone to extinction whereas species that are characterized by both high abundance and wide distributions are less prone to extinction (Gaston 1998, Johnson 1998). The positive relationship between local abundance and distribution holds for recent species, thereby providing insight into

the factors that affect extinction and highlighting the importance of phylogenetic control for maintaining the relative independence of data points as well as the value of the comparative method for uncovering macroecological patterns (Gaston 1998).

Relationship between range size and body size

Another relevant pattern regarding the distribution and abundance of species is the apparent interspecific relationship between body size and geographic range size. Among congeneric or otherwise closely related animals, the most widespread species tend to have the largest body size, on average (Averill 1933, Brown 1981, Brown and Gibson 1983, Brown and Maurer 1987). Some authors (Brown 1981, Brown and Gibson 1983, Brown and Maurer 1987) have suggested that minimum viable geographic range scales positively with body size. Larger species have larger home ranges and lower densities (Peters 1983), resulting in smaller local populations. Large species with both small local populations and small geographic ranges would have small total regional populations and a higher probability of extinction (Gaston 1998, Johnson 1998). Curiously, the positive correlation between body size and geographic range size does not hold for kangaroo rats (Fig. A.3). There is not a significant correlation between geographic range size and mean adult body mass ($r_s = -0.321$, $P = 0.365$, $n = 10$); in fact, the three largest geographic ranges are held by some of the smallest species for which mean adult body masses were available in the literature (Jones 1985). Gaston (1988b) recognized that intrinsic rate of increase, r , typically scales negatively with body size and suggested that smaller species may therefore be better able to expand their ranges (colonize sites) than larger species because smaller species are less vulnerable to stochastic extinction as they rapidly attain viable population sizes (Mayr 1963,

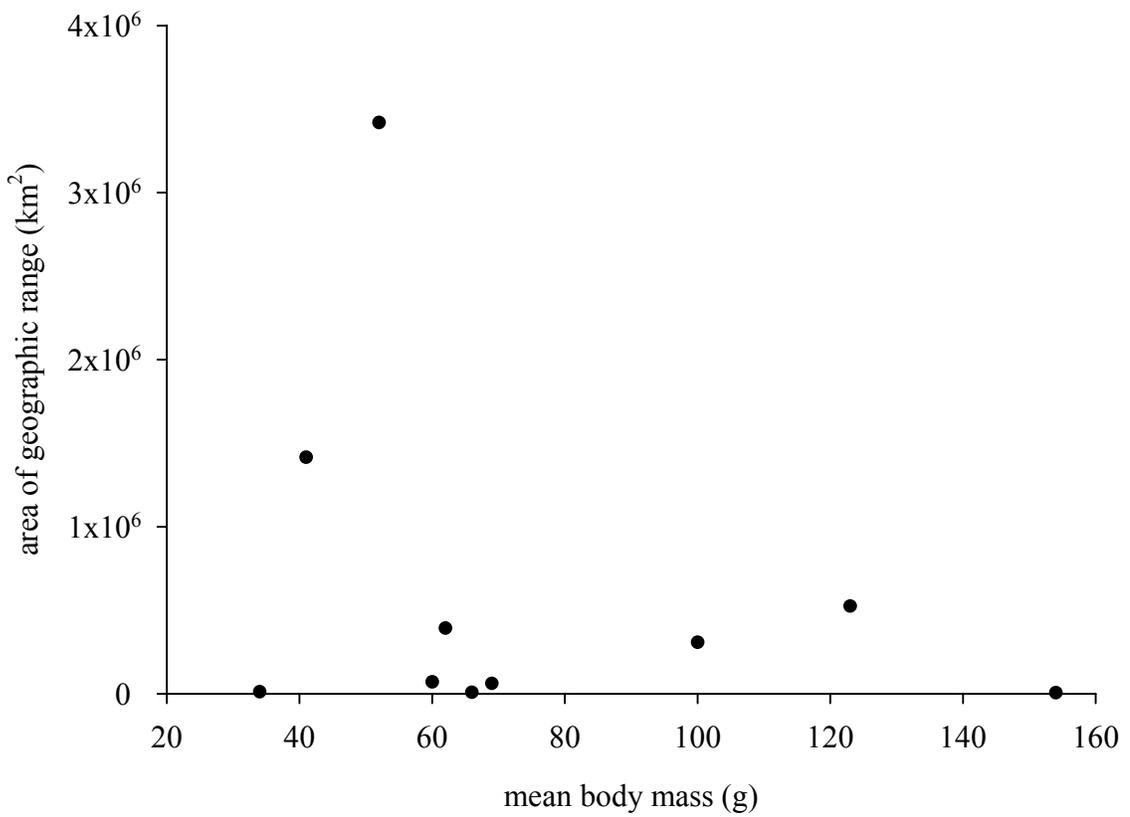


Figure A.3 Bivariate plot of body size versus total area of geographic range for 10 species of kangaroo rats for which mean adult body masses were available in the literature (after Jones 1985).

MacArthur and Wilson 1967). Relative to other small mammals, kangaroo rats typically have low intrinsic rates of increase and high longevity (Kenagy and Bartholomew 1985, Brown and Harney 1993). This life history strategy is thought to be appropriate given the irregularity of favorable environmental conditions in desert environments (Kenagy and Bartholomew 1985, Brown and Harney 1993). This general life history strategy may partially explain why large kangaroo rats do not have large ranges and why smaller kangaroo rats, with marginally higher intrinsic rates of increase, might tend to have attained large geographic range sizes more successfully. Furthermore, the large species of kangaroo rats that have low intrinsic rates of increase and small geographic ranges should be particularly susceptible to stochastic events and prone to extinction.

Intraspecific distribution of abundance

General patterns regarding the intraspecific distribution of abundance are highly relevant to analyses of the apparent persistence of peripheral populations because they are the basis of the demographic hypothesis that peripheral populations should be more prone to extinction than more central populations (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b). The traditional view of intraspecific variation in abundance across species ranges was that abundance declines from central regions to the peripheries (Grinnell 1922, Andrewartha and Birch 1954, Udvardy 1969). Subsequently, the distribution of abundance within species geographic ranges was likened to a bivariate normal density function (Hengeveld and Haeck 1982, Brown 1984), centred about the mean which is approximately the centre of the species geographic range, with abundance declining towards the peripheries. Brown (1984) proposed that the observed geographical pattern

of abundance is generated when many different factors with additive effects, akin to the multidimensional niche concept (Hutchinson 1957), are spatially autocorrelated and combine to affect population density. The centre of the geographic range should be the location where the combination of all these factors is optimal and should be characterized by the highest abundance for the species (Brown 1984). A true bivariate normal density surface for abundance is unlikely for most species, given natural landscape heterogeneity; however, multiple locations of peak abundance (i.e., multi-modal density surfaces), as well as abrupt changes in abundance can also be explained according to the theory of spatially autocorrelated factors with additive effects (Brown 1984).

Brown et al. (1995) further confirmed the general pattern of decline in abundance towards the peripheries through their studies of North American Breeding Bird Survey data, but revised the theory regarding the distribution of abundance, given that, species tended to occur at extremely high densities in only a few “hot spots” whereas they were orders of magnitude less abundant elsewhere in their ranges. Brown et al. (1995) concluded that the amount of spatial autocorrelation in environmental factors had been severely overestimated by previous researchers (Hengeveld and Haack 1982, Brown 1984, Hengeveld 1989). Although the distribution of abundance is not necessarily as straightforward as fitting a bivariate normal density function, it is still a useful analogy: for any particular species, the distribution of abundance may not follow a bivariate normal density surface, but on average among many species, there is likely to be a strong central tendency for abundance, accompanied by declines in abundance towards the peripheries.

The concept of abundance being greatest near the centre of species ranges and declining towards the peripheries (Grinnell 1922, Andrewartha and Birch 1954, Udvardy 1969, Hengeveld and Haeck 1982, Brown 1984, Brown et al. 1995) has been so broadly accepted that it has been denoted as a general rule of biogeography (Hengeveld and Haeck 1982, Brown and Gibson 1983, Hochberg and Ives 1999), though it has also more recently been referred to as the abundant-centre hypothesis (Sagarin and Gaines 2002). A review of published evidence for the abundant-centre hypothesis found that only 39 % (n = 145) of statistical tests in empirical studies reported direct evidence in favor of the abundant-centre hypothesis, according to a simple vote-counting analysis (Sagarin and Gaines 2002). Sagarin and Gaines (2002) also reviewed a relatively small number of indirect tests (n = 28) of the abundant-centre hypothesis, in which previous authors had examined ecological or evolutionary expectations based on abundant-centre distributions—for example, the unexpected persistence of peripheral populations (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b). Overall, these indirect tests of the abundant-centre hypothesis did not support or discount the hypothesis (Sagarin and Gaines 2002). There was no significant difference between the numbers of indirect studies that appeared to support the abundant-centre hypothesis (46 %, n = 13), did not appear to support the abundant-centre hypothesis (25 %, n = 7), or were inconclusive (29 %, n = 8; Sagarin and Gaines 2002). The authors also concluded that remarkably few studies had adequately sampled species geographic ranges (Sagarin and Gaines 2002). Clearly, overwhelming evidence for the abundant-centre hypothesis regarding the intraspecific distribution of abundance is lacking. Thorough, systematic sampling and analyses of species ranges with particular emphasis on the peripheries (Sagarin and Gaines 2002),

perhaps through large-scale collaborations, will be required to better evaluate this macroecological pattern before it should be considered a general rule of biogeography. Yet, despite this potential uncertainty, the abundant-centre distribution provides the underlying rationale for the demographic hypothesis that predicts persistence of species in central regions as opposed to the peripheries (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b).

What makes a population peripheral?

General patterns regarding the overall distribution and abundance of species are highly relevant to species declines, collapses of geographic ranges, and the apparent persistence of peripheral populations. The literature regarding the distribution and abundance of species is laden with usage of the term “peripheral”. Its usage may be frequent, but generally it is unsatisfactorily defined. To my knowledge, there has never been an explicit recommendation for a particular means of quantifying peripherality, aside from *de facto* endorsement by publication of subsequent analyses (e.g., see Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b).

Ideally, for any one particular population of a species, the relative degree of peripherality should be ascertained according to detailed knowledge of life history (e.g., dispersal capabilities, home range size, longevity), population genetics, and local distribution and abundance. Such data are usually difficult to acquire, as evidenced by the scarcity of studies that adequately sample local abundance across species’ entire geographic ranges (Sagarin and Gaines 2002). As a result, such detailed data are not often employed in the majority of macroecological analyses. The trend among

macroecologists is to study large-scale and multi-species patterns for the purposes of inferring underlying, broad-scale ecological processes (Brown 1995, Blackburn and Gaston 2002, Nee 2002), usually at the expense of incorporating detailed information on particular populations.

Strictly in the context of macroecology, then, if it is accepted that detailed species and site-specific knowledge are not prerequisite for understanding general patterns among species, then it still must be asked: what exactly is meant by peripherality? There has been no technical formulation in the literature and authors that have referred to peripherality either did not define it explicitly (e.g., Wolf et al. 1996) or assigned peripherality for subsequent analyses using varying techniques (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b).

According to Lesica and Allendorf (1995:753), a simple conceptual definition of peripheral populations is that “strictly speaking, peripheral populations are separated from central ones by spatial distance”. Instead, however, other authors defined peripherality operationally according to distance from the edges of geographic ranges (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000b). They calculated an index of centrality, the opposite of peripherality, for which the half of the species range that is furthest from the edge (greater than the median distance from the edge) was designated as central whereas the half that was closest to the edge was considered peripheral (henceforth median edge-distance model; Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000b). For reference, I estimated the size and distribution of the peripheries for kangaroo rats according to the median edge-distance method (Fig. A.4). I found that the median edge-

distance method is a convenient estimation of peripherality because it is simple, binary, and separates geographic ranges into areas of equal size, theoretically enabling straightforward null hypotheses (50 %) against which to test for potential patterns. However, there are a number of shortcomings of this model of peripherality. First, it would seem more reasonable to expect that peripheral populations should be exceptional as opposed to common. The median edge-distance approach implicitly considers that (by area) peripheral populations are equally as common as more central populations—surely this definition is too liberal. The median edge-distance model also assumes that peripherality is truly binary. For the majority of analyses (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000b), the index of centrality was used to designate regions as either central or peripheral (with respect to historical distributions) irrespective of varying degrees of peripherality. Perhaps even more telling, are maps of central and peripheral regions according to the median edge-distance method (Fig. A.4). Figure A.4 illustrates that, according to the median edge-distance model: (i) the peripheries are equally as large as central regions; and (ii) for species distributions with naturally irregular, complex shapes, many regions are categorized as peripheral even though they are much nearer to the centre than are other regions that are classified as central. Although a number of published studies have used the median edge-distance model of peripherality (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000b), I suggest that this model is too liberal and not logically consistent with the concept of peripherality.

In a more frequently cited study, Channell and Lomolino (2000a) adopted an operational definition of centrality and peripherality that differed from the previous method. They classified the region that was located more than half the maximum

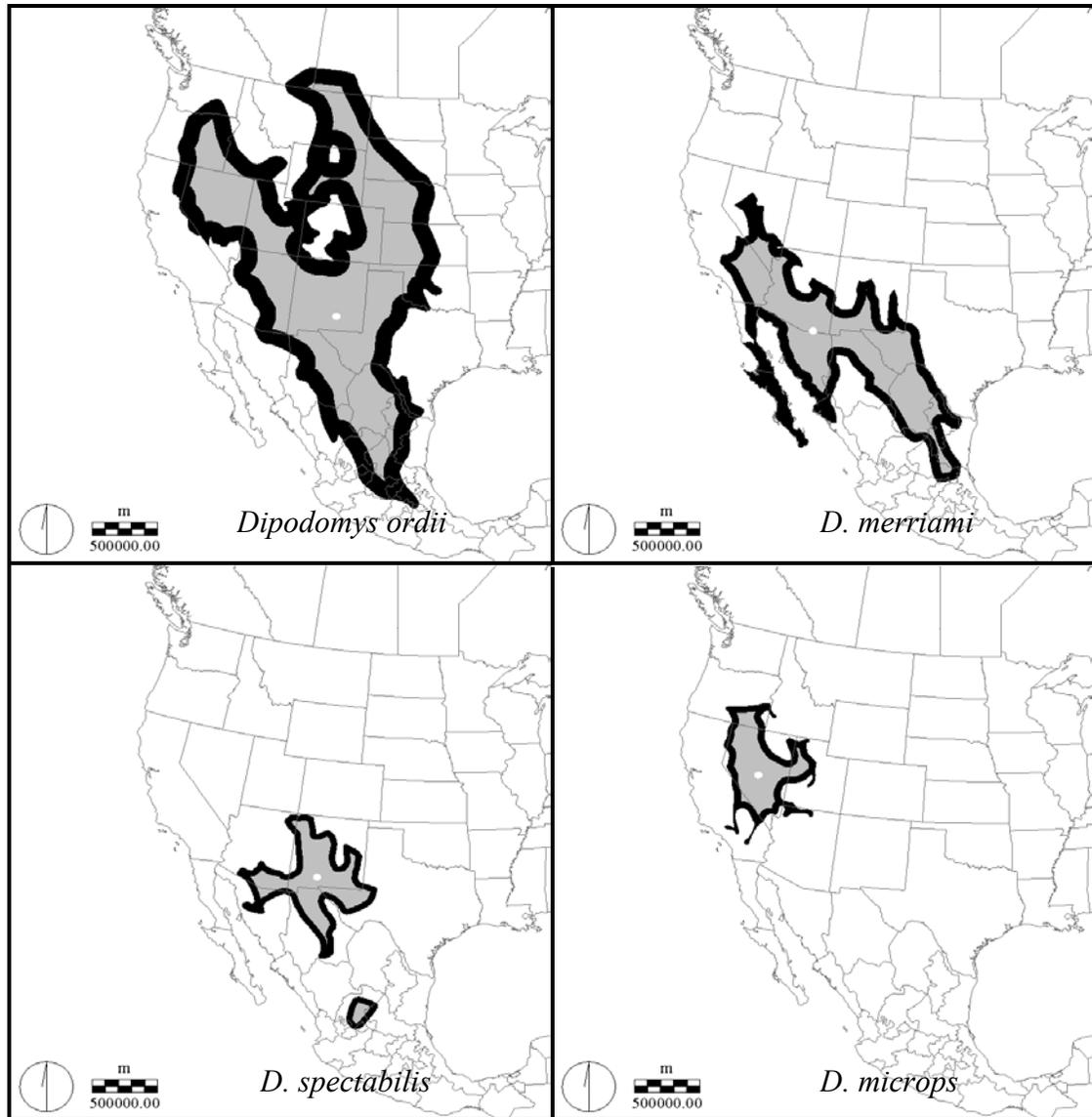


Figure A.4 Maps of the distributions of peripheral and central regions for the geographic ranges of four species of kangaroo rats, according to the median edge-distance method (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000b). The black region was classified as the periphery whereas the grey region was classified as the central region. The centre of the species distribution is shown with a white point symbol.

distance from the range limits as central and the remainder as peripheral (henceforth half edge-distance model; Channell and Lomolino 2000a). Unfortunately, the half edge-distance method does not provide a better estimate of peripherality than the median edge-distance method because as geographic range size increases or as the size of the final or extant range decreases (i.e., the greater the range collapse), there is an increasing bias towards the peripheries.

To demonstrate this bias, I quantified the area of the peripheral regions according to the two different techniques (median edge-distance versus half edge-distance methods) for the geographic ranges of kangaroo rats (Figs. A.4 and A.5). I found that the half edge-distance method caused the relative size of the peripheries to increase drastically due to an “area effect” (Table A.1 and Fig. A.6). That is, if one considers a species that is distributed across a circular geographic range: for each increase in the size of the radius by a factor of R , the total area increases by a factor of R^2 . This intrinsic bias would not have been critical for the analyses by Channell and Lomolino (2000a) except that, by the very purpose and nature of the study, the authors were comparing historical and extant ranges for species that had declined to small (< 25 %) proportions of their ranges. The larger the historical distribution and the smaller the extant distribution, the less likely the extant range was to contain any central region purely as a function of the operational definition of the peripheries.

If the geographic ranges of kangaroo rats are reasonably representative of the sizes and shapes of typical geographic ranges, then the average relative size of the peripheries would be approximately 74 % of total range size (Table A.1). Channell and Lomolino (2000a) reported that 68 % ($n = 245$) of species persisted more in the

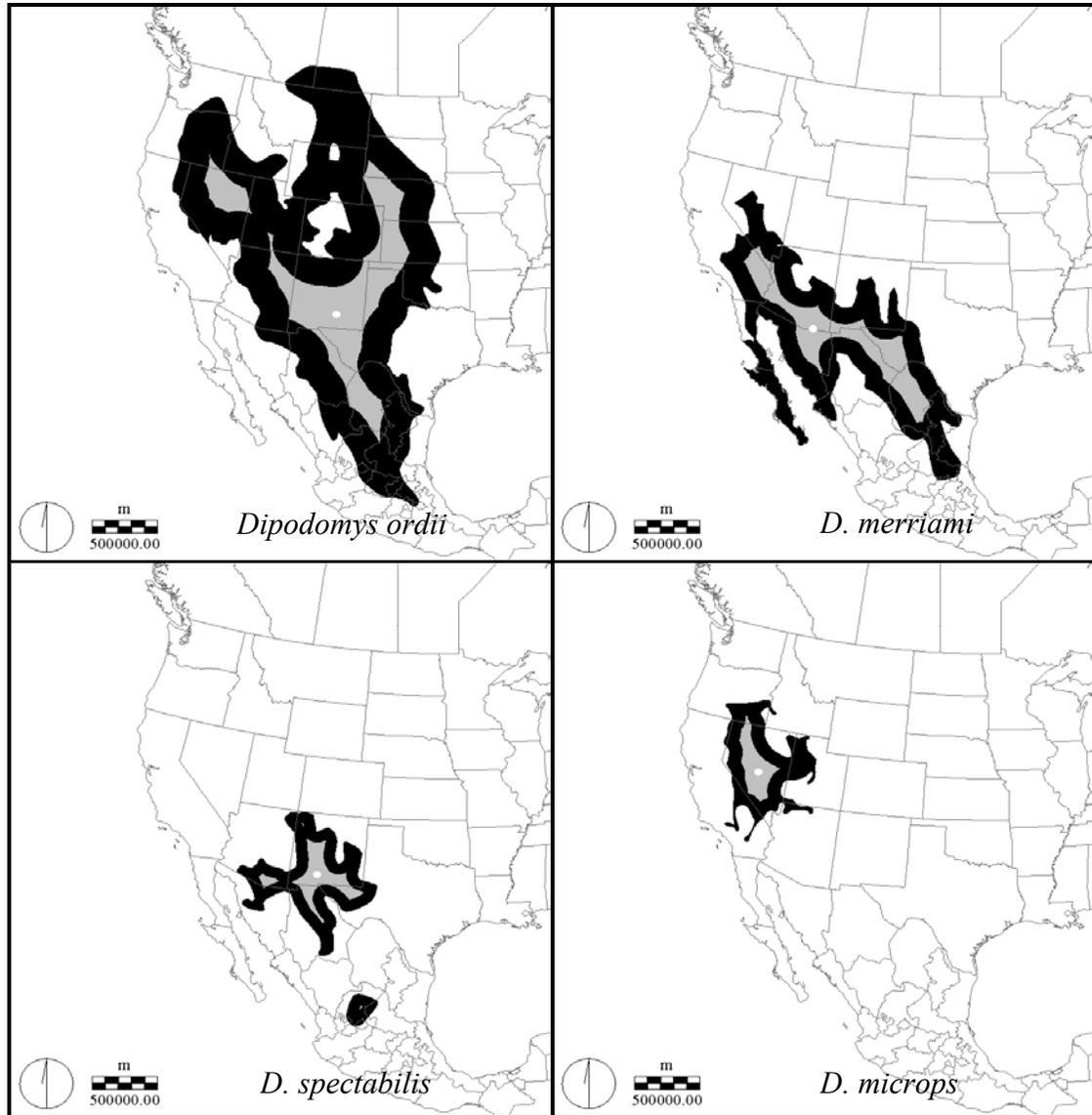


Figure A.5 Maps of the distributions of peripheral and central regions for the geographic ranges of four species of kangaroo rats, according to the half edge-distance method (Channell and Lomolino 2000a). The black region was classified as the periphery whereas the grey region was classified as the central region. The centre of the species distribution is shown with a white point symbol.

peripheries than in central regions of their geographic ranges, according to the half-distance method. A coarse adjustment for the underlying bias towards the peripheries would have been to adjust the null hypothesis (they used 50 %) for the binomial test according to the average overrepresentation of the peripheries. This adjustment to the null hypothesis (74 %) would have changed their results to indicate that species persisted in the peripheries slightly less often than expected by chance ($P = 0.024$, binomial test), potentially negating the significance of the peripheries and possibly strengthening the argument that species ranges may tend to contract away from the peripheries. However, I cannot be sure of the appropriate adjustment to the null hypothesis for their particular dataset. Therefore, I cannot necessarily negate the reported pattern of disproportionate persistence in the peripheries—which, notably, had also been reported based on the median edge-distance model of peripherality (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000b) which fortunately does not suffer from the same inherent bias. I simply contend that both previous, quantitative definitions of peripherality were inadequate because they were not logically consistent with the concept of peripherality. Therefore, I seek to develop a new and more appropriate quantitative definition of peripherality, which is elaborated below.

Redefining peripheral populations

To provide an improved, quantitative model of peripherality, it is worth considering the fundamental characteristics that make peripheral populations distinct. I suggest that the following two traits are the underlying, primary factors that contribute to the peripherality of a population:

- (i) Differences in significant biotic or abiotic environmental factors that affect population viability, as compared to central populations;
- (ii) Reduced connectivity of populations for immigration/emigration, resulting in reproductive isolation and potential for micro-evolutionary divergence.

Local abundance and variation thereof are not necessarily definitive characteristics of peripheral populations; they are instead expectations of the abundant-centre hypothesis (Grinnell 1922, Andrewartha and Birch 1954, Udvardy 1969, Hengeveld and Haeck 1982, Brown 1984, Brown et al. 1995, Sagarin and Gaines 2002). I submit that, in lieu of detailed life history and local distribution and abundance information, Euclidean distance may serve as a useful index of both (i) differences in environmental factors, and (ii) connectedness of populations.

Both previous quantitative techniques for estimating peripherality (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b) were binary classifications that were based on Euclidean distance from the nearest edge of the geographic range. Similarly, peripherality could be defined strictly according to distance from the nearest edge but on a continuous scale. Would a continuous edge-distance model be more appropriate than the previous median edge-distance or half edge-distance models? For example, the edge-distance model of peripherality could represent the relative peripherality (P) of a location or population as:

$$P = 1 - \frac{D_E}{MaxD_E} \quad (\text{A.1})$$

where D_E is the Euclidean distance from the nearest edge. As such, locations that are closest to an edge would have an estimated peripherality that approaches $P = 1$ whereas

those locations that are nearest to centre (the maximum distance from any edge $MaxD_E$) would have an estimated peripherality that approaches $P = 0$. Figure A.7 shows the distributions of four species of kangaroo rats according to the continuous edge-distance model. The simple improvement that is inherent in this model is that it provides a continuous index that imparts more information regarding the relative degree of peripherality than does a binary or categorical value. However, if necessary, this model of peripherality could easily be generalized to provide a categorical distribution by simply defining a threshold value for distinguishing peripheral versus central regions. The continuous-scale edge-distance model would be an improvement over both previous (categorical) models. However, the edge-distance model may not adequately capture the two defining traits of peripherality: differences in environmental parameters and segregation from more central populations. Figure A.7 reveals that there would be many locations that are close to an edge and hence considered highly peripheral, yet are also closer to the centre than many other locations that are estimated as less peripheral. Although the edge-distance model of peripherality is useful due to its continuous scale, it probably does not sufficiently represent the relative peripherality of a location or population.

Any model of peripherality that is based strictly on distance from the nearest edge would be inconsistent with the definition that was provided by Lesica and Allendorf (1995). Conceptually, peripheral populations should be defined by spatial separation from more central populations (Lesica and Allendorf 1995). Therefore, would distance from the centre, in and of itself, provide an improved model of peripherality? Peripherality (P) could be estimated according to a centre-distance model:

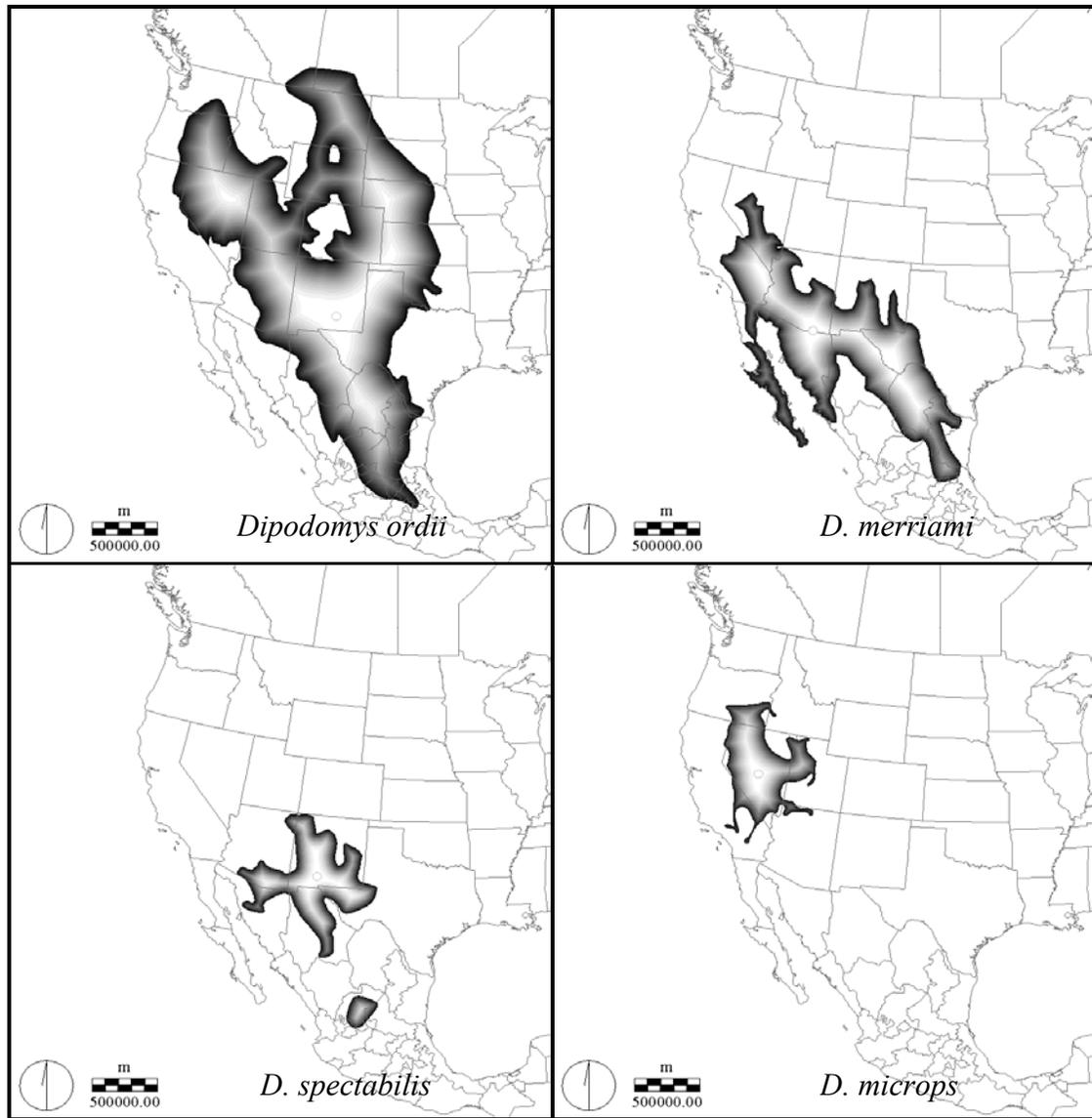


Figure A.7 Maps of relative peripherality for the geographic ranges of four species of kangaroo rats according to the edge-distance model. The darker the region, the higher the index of peripherality. The centre of the species distribution is shown with a white point symbol.

$$P = \frac{D_C}{MaxD_C} \quad (A.2)$$

where D_C is the distance from the centre of the species geographic range. Figure A.8 shows the distributions of four species of kangaroo rats according to the centre-distance model. The centre-distance model also provides the benefit of a continuous variable and could be ranked and compared ordinally. Again, it could be extended, as necessary, to any categorization according to percentile values or other arbitrary thresholds if required for testing patterns against particular null hypotheses. More importantly, however, the centre-distance model is logically consistent with the previous conceptual definition of peripheral populations (Lesica and Allendorf 1995). However, depending on the shape of the species distribution, there would still be locations that occur immediately at the edge of the species range yet are considered less peripheral than other locations that are distant from the centre but do not occur near the edge of the species range.

I propose that neither distance from centre, nor distance from edge, is more important than the other in describing relative degree of peripherality: both should be weighted equally. Only for a hypothetical species that is distributed across a perfectly circular geographic range, would the relative peripherality of a location truly be a function of how close it is to the edge (perimeter of the circle) or equally, how distant it is from the centre. In the special case of a perfect circle, these two models are interchangeable. However, consider a hypothetical species range that is more elliptical than circular. Should the most distant edges (at the intersection of the major axis and the perimeter) be considered equally peripheral, or more peripheral, than the points along the edges that are nearest to the centre (at the intersection of the minor axis and the

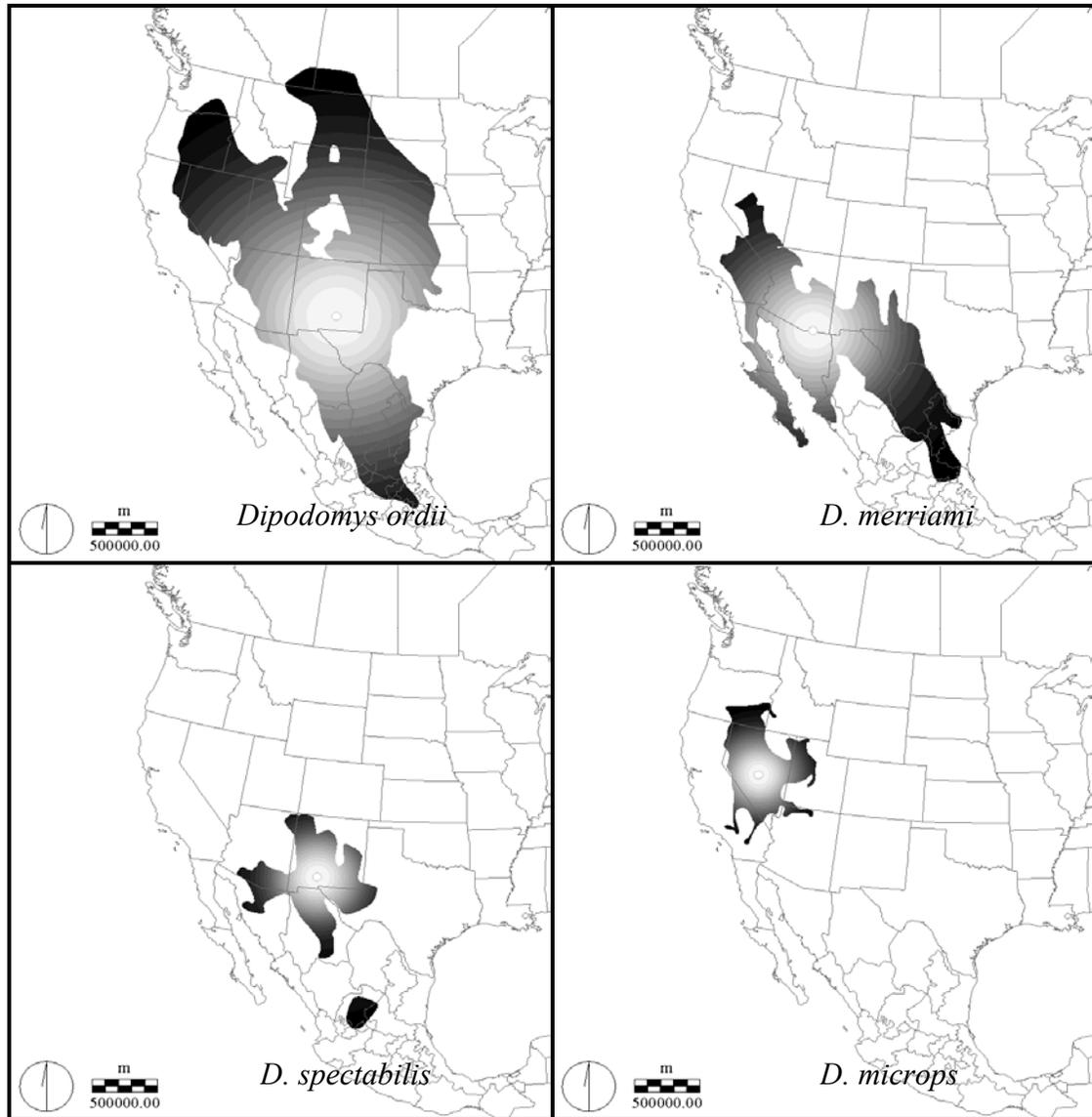


Figure A.8 Maps of relative peripherality for the geographic ranges of four species of kangaroo rats according to the centre-distance model. The darker the region, the higher the index of peripherality. The centre of the species distribution is shown with a white point symbol.

perimeter)? An improved model of peripherality should adequately capture the relative peripherality of distributions regardless of the particular shapes of those distributions. Yet, this simplistic comparison of circular and elliptical distributions illustrates that an improved model of peripherality should incorporate information about both: (i) proximity to the edge, where environmental conditions would usually be most different from the centre and nearest to those extremes that delimit population viability; and (ii) distance from the centre, as another equally important index of similarity for spatially autocorrelated factors such as environmental conditions, as well as population connectivity or genetic relatedness. Hence, I propose the following weighted-distance model for estimation of peripherality (P):

$$P = \frac{\left(1 - \frac{D_E}{MaxD_E}\right) + \frac{D_C}{MaxD_C}}{2} \quad (\text{A.3})$$

where D_E is the distance from the nearest edge and D_C is the distance from the centre. Peripherality (P) would range from $P = 0$ at the centre of the species geographic range ($MaxD_E$) to $P = 1$ at any point that is both closest to the edge and furthest from the centre ($MaxD_C$). Figure A.9 shows the distributions of four species of kangaroo rats according to the weighted-distance model. The weighted-distance model also provides a continuous variable which could be ranked and compared on an ordinal scale. Again, it could be generalized to any categorization for analyses and interpretation, such as percentile bands or a binary categorization if necessary for testing patterns against certain null hypotheses. More importantly, it would be logically consistent with the previous conceptual definition of peripheral populations, by incorporating information about distance from the centre (Lesica and Allendorf 1995), as well as the previous

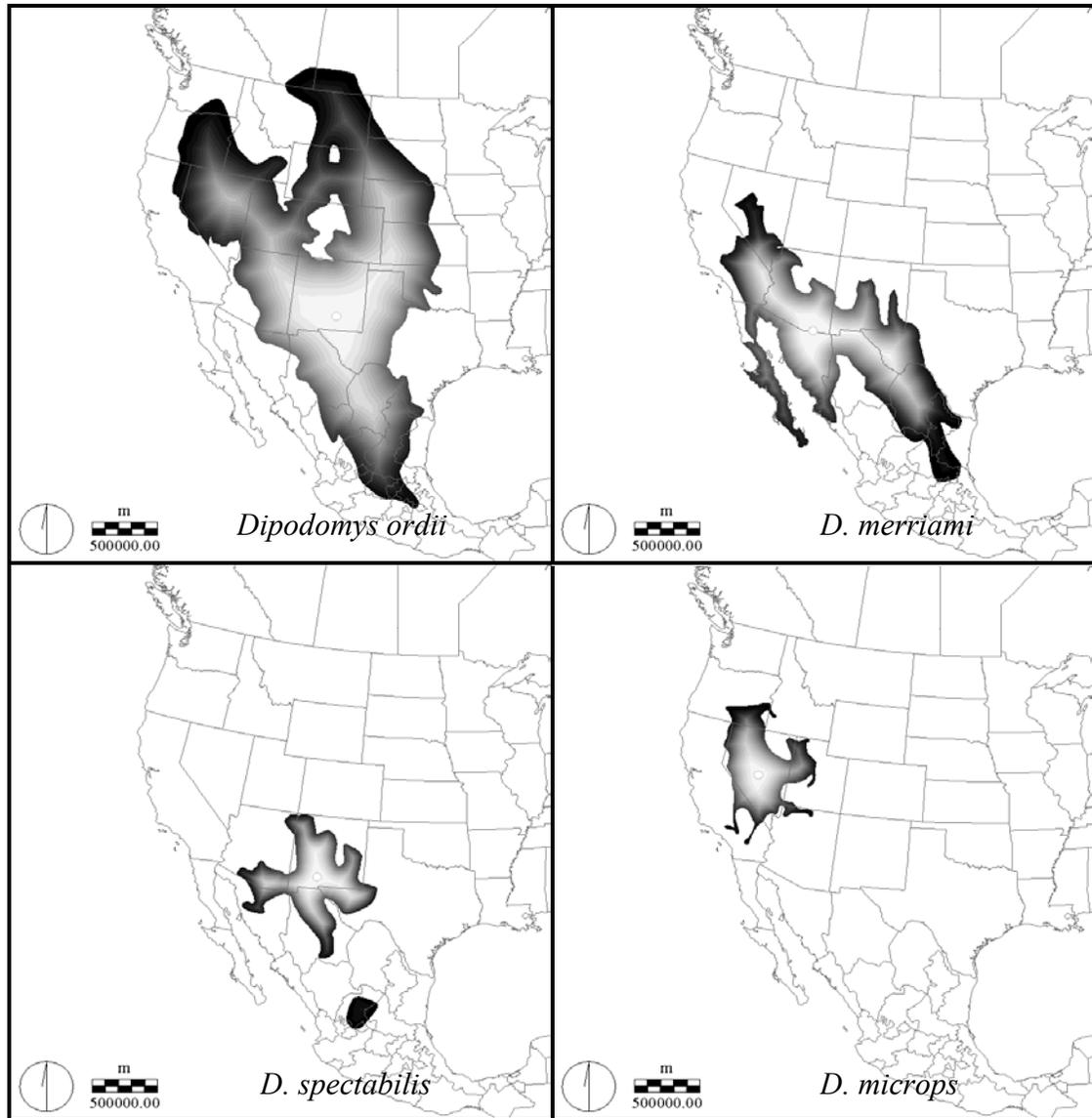


Figure A.9 Maps of relative peripherality for the geographic ranges of four species of kangaroo rats according to the weighted-distance model. The darker the region, the higher the index of peripherality. The centre of the species distribution is shown with a white point symbol.

operational definitions of peripherality according to distance from the edge (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b). Regardless of the particular shape of any distribution, the relative peripherality of any location could be determined as a function of both distance from edge and distance from centre, thereby preventing outright logical inconsistencies. There would still be locations at the range limits that are not considered highly peripheral, but only if they are extremely close to the centre; similarly, there would still be sites that are considered relatively peripheral even if they do not occur close to an edge, but only if they are extremely distant from the centre. I suggest that the weighted-distance model provides important improvements over previous conceptual and operational models of peripherality.

An empirical evaluation of peripherality

I examined the relative effectiveness and potential for biases of the weighted-distance model versus previous and alternative models by applying each model to the distributions of kangaroo rats. For each species, I simulated a complete range collapse that left a persistent population at only one site within its former range. I replicated this simulation 100 times by overlaying 100 random point locations as simulated “final sites” within each species range. To be consistent with the analytical methods used by previous studies (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b), I applied simple binomial tests against binary extensions of each (continuous) model to quantify the apparent persistence of the random final sites. Specifically, I compared the following models:

- (i) Median edge-distance model

- (ii) Half edge-distance model
- (iii) 25th percentile edge-distance model
- (iv) 25th percentile centre-distance model
- (v) 25th percentile weighted-distance model

Figures A.10 and A.11 show the distributions of the peripheral and central regions according to each of the above models of peripherality for Ord's and Merriam's kangaroo rats, respectively. As predicted, the half edge-distance method (Channel and Lomolino 2000a) defines the majority of randomly chosen sites as peripheral (Table A.2). However, none of the other methods showed bias (Table A.2). Qualitative examinations of Figures A.10 and A.11 support the expectation that the weighted-distance model provides the best combined representation of proximity to the edge and distance from centre.

Discussion

I have examined the operational and analytical definitions of peripherality, and demonstrated that current quantitative methods for defining peripheral populations are inadequate. Based on this information, I have developed and evaluated an improved, quantitative and operational model of peripherality that can be used for estimation of peripherality and analyses of biogeographical patterns with respect to peripheral populations. The weighted-distance model represents the two fundamental traits that make peripheral populations distinct because it incorporates information regarding both: (i) proximity to the edge, where environmental conditions would usually be most different from the centre, and nearest to those extremes that delimit population viability;

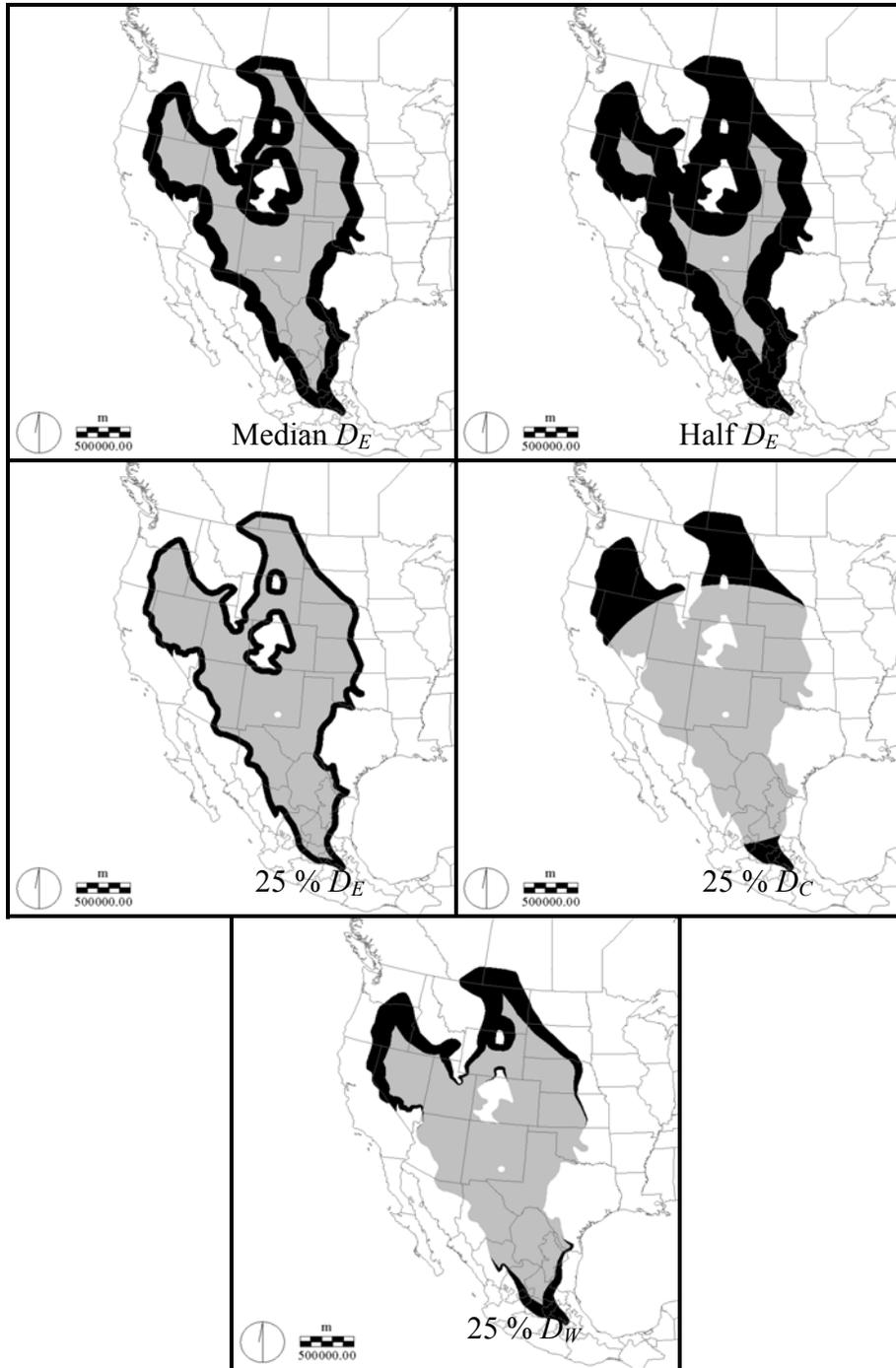


Figure A.10 Maps of the distributions of peripheral and central regions for the geographic range of Ord's kangaroo rats according to alternative methods of estimating the peripheries: (i) median edge-distance model; (ii) half edge-distance model; (iii) 25th percentile edge-distance model; (iv) 25th percentile centre-distance model; and (v) 25th percentile weighted-distance model. For each model, the black region was classified as the periphery whereas the grey region was classified as the central region. The centre of the species distribution is shown with a white point symbol.

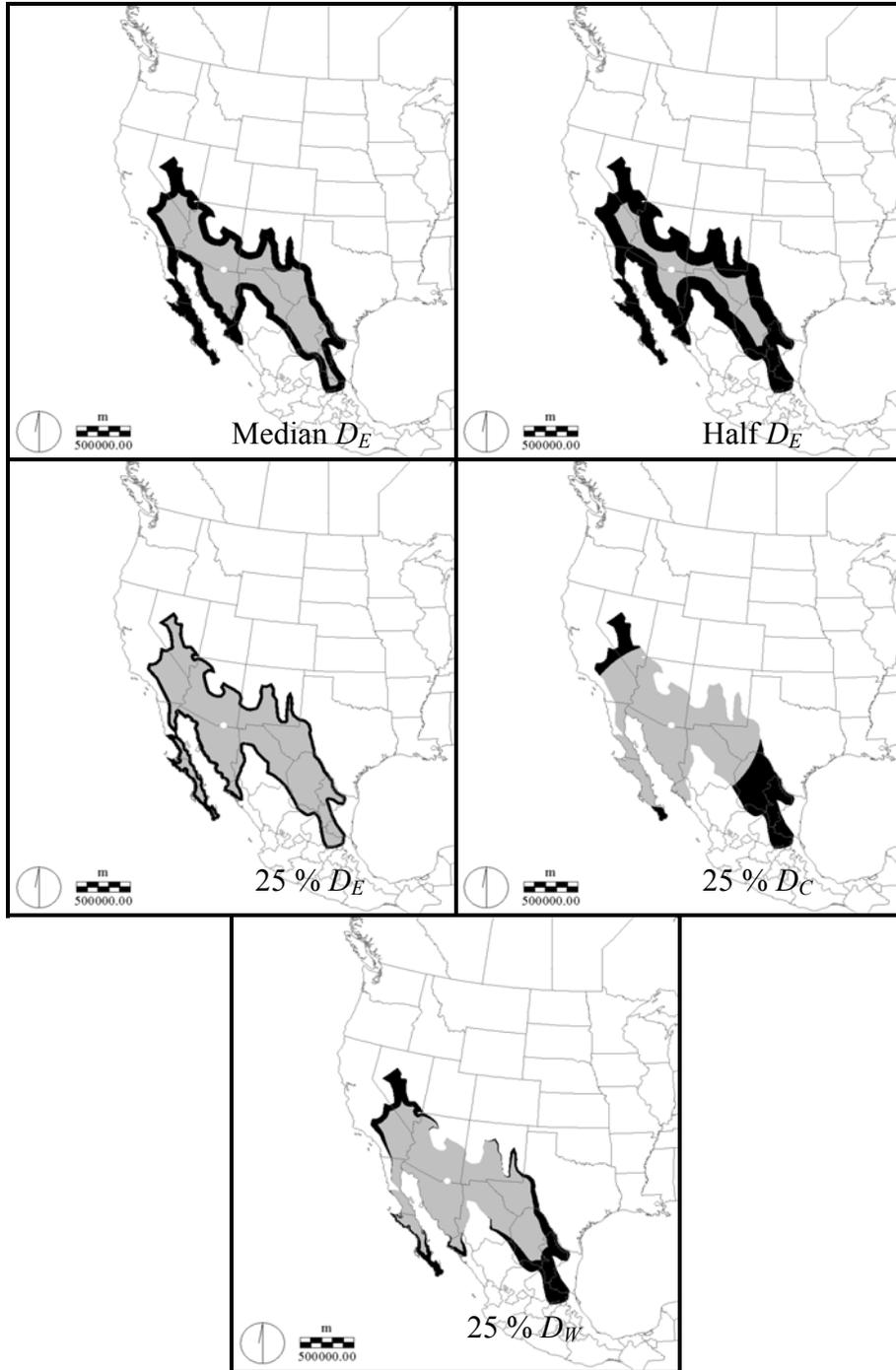


Figure A.11 Maps of the distribution of peripheral and central regions for the geographic range of Merriam's kangaroo rats according to alternative methods of estimating the peripheries: (i) median edge-distance model; (ii) half edge-distance model; (iii) 25th percentile edge-distance model; (iv) 25th percentile centre-distance model; and (v) 25th percentile weighted-distance model. For each model, the black region was classified as the periphery whereas the grey region was classified as the central region. The centre of the species distribution is shown with a white point symbol.

Table A.2 Numbers of randomly generated locations that were assigned to the peripheries of distributions of kangaroo rats according to five different methods of estimating peripherality: the median edge-distance model (Median D_E), half edge-distance model (Half D_E), 25th percentile edge-distance model (25 % D_E), 25th percentile centre-distance model (25 % D_C), and 25th percentile weighted-distance model (25 % D_W). Asterisks indicate significant* ($P < 0.05$) and highly significant** ($P < 0.01$) differences from expected values according to simple binomial tests. The Median D_E and Half D_E models were tested against a null hypothesis of 50 % as per Channell and Lomolino (2000a, 2000b) whereas the other (new) models were tested against a null hypothesis of 25 %.

| Scientific name | Median D_E | Half D_E | 25 % D_E | 25 % D_C | 25 % D_W |
|-------------------------|--------------|------------|------------|------------|------------|
| <i>Dipodomys agilis</i> | 55 | 76** | 27 | 28 | 29 |
| <i>D. californicus</i> | 56 | 75** | 25 | 28 | 30 |
| <i>D. compactus</i> | 51 | 66** | 25 | 29 | 27 |
| <i>D. deserti</i> | 40 | 68** | 18 | 22 | 25 |
| <i>D. elator</i> | 51 | 64** | 23 | 25 | 25 |
| <i>D. gravipes</i> | 46 | 78** | 23 | 29 | 28 |
| <i>D. heermanni</i> | 54 | 90** | 25 | 21 | 26 |
| <i>D. ingens</i> | 46 | 77** | 29 | 28 | 24 |
| <i>D. insularis</i> | 42 | 73** | 2** | 27 | 25 |
| <i>D. margaritae</i> | 61* | 60 | 21 | 17 | 13* |
| <i>D. merriami</i> | 54 | 80** | 32 | 28 | 27 |
| <i>D. microps</i> | 56 | 80** | 26 | 25 | 30 |
| <i>D. nelsoni</i> | 43 | 66** | 14* | 15* | 15* |
| <i>D. nitratoides</i> | 51 | 73** | 26 | 22 | 14* |
| <i>D. ordii</i> | 44 | 82** | 20 | 29 | 23 |
| <i>D. panamintinus</i> | 46 | 75** | 24 | 26 | 30 |
| <i>D. phillipsii</i> | 46 | 66** | 29 | 26 | 24 |
| <i>D. simulans</i> | 46 | 63* | 20 | 29 | 25 |
| <i>D. spectabilis</i> | 46 | 77** | 23 | 30 | 26 |
| <i>D. stephensi</i> | 55 | 73** | 26 | 30 | 25 |
| <i>D. venustus</i> | 52 | 82** | 28 | 26 | 28 |
| Mean | 50 | 74 | 23 | 26 | 25 |
| Standard error | 1.2 | 1.6 | 1.4 | 0.9 | 1.1 |

and (ii) distance from the centre, as another equally important index of similarity for spatially autocorrelated factors such as environmental conditions, as well as population connectivity or genetic relatedness. I recommend that the weighted-distance model should be used to re-evaluate the apparent persistence of peripheral populations of a wide range of taxa for which maps of geographic range collapses have already been compiled (e.g., Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b). It has been difficult to convince conservation biologists that the peripheries warrant substantial conservation efforts, given the limited successes of some conservation programmes in the peripheries (Griffith et al 1989, Wolf et al. 1996) and the traditional expectation that peripheral populations should collapse before central populations (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b). However, if the previously reported biogeographical pattern of persistence near the peripheries is robust to this new and more logically consistent definition of the peripheries, then it will reinforce the importance of peripheral populations and assist in prioritization of conservation efforts for endangered species and global biodiversity. I do not discount the conclusions of previous studies that adopted different models of peripherality (e.g., Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b) because there are several reasons to expect peripheral populations to contribute disproportionately more to the persistence of species through periods of perturbation or gradual environmental change.

Theory of persistence of peripheral populations

Channell and Lomolino (2000a, 2000b) noted that the tendency for species geographic ranges to collapse towards the peripheries differs from the pattern that would be predicted according to traditional perspectives on demographic processes (Grinnell 1922, Andrewartha and Birch 1954, MacArthur and Wilson 1967, Udvardy 1969, Goel and Richter-Dyn 1974, , Brown and Kodric-Brown 1977, Hengeveld and Haeck 1982, Rapoport 1982, Brown and Gibson 1983, Brown 1984, Pimm et al. 1988, Gaston 1990, Hengeveld 1990, Tracy and George 1992, Maurer 1994, Brown et al. 1995, Lawton 1995, Hochberg and Ives 1999). They reported that this biogeographical pattern was indicative of the contagion-like spread of extrinsic forces of extinction (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b). Populations near the peripheries, or in other isolated, insular habitats should be the last to be affected by extrinsic forces of extinction, and should therefore be expected to persist the longest (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b). As evidence in support of this theory, Channell and Lomolino (2000a) noted that only two geographic regions yielded outliers from this observed tendency for peripheral persistence: (i) Africa, where human disturbance occurred over substantially more time than in other areas (Martin 1984); and (ii) Hawaii, where humans colonized the peripheral coastal lowlands forcing remnant populations of native species into montane centres of the islands (Channell and Lomolino 2000a). However, the authors (Channell and Lomolino 2000a, Channell and Lomolino 2000b) did not explicitly acknowledge the possibility that other, inherently biological considerations could also contribute to the overall consistent patterns of geographic range collapses towards the peripheries.

I suggest that demographic and contagion-like processes (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b) should not be considered mutually exclusive and that there are several reasons to expect persistence of peripheral populations. I propose that there are at least three reasons why the extrinsic, contagion hypothesis should not be considered the only logical explanation of persistence of some peripheral populations: (i) dynamic abundant-centre; (ii) correlation between demography and contagions; and (iii) population diversity.

First, the underlying principles of the demographic hypothesis (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b) are the abundant-centre distribution (Grinnell 1922, Andrewartha and Birch 1954, Udvardy 1969, Hengeveld and Haeck 1982, Rapoport 1982, Brown and Gibson 1983, Brown 1984, Gaston 1990, Hengeveld 1990, Maurer 1994, Brown et al. 1995, Lawton 1995, Hochberg and Ives 1999, Sagarin and Gaines 2002) and extensions of island biogeography theory (MacArthur and Wilson 1967, Goel and Richter-Dyn 1974, Brown and Kodric-Brown 1977, Pimm et al. 1988, Tracy and George 1992). However, I argue that the demographic hypothesis as stated previously (Channell and Lomolino 2000a, Channell and Lomolino 2000b) does not sufficiently acknowledge changes with respect to demography through time. A more dynamic hypothesis according to demographic processes should be cognizant that the particular locations of the prerequisite abundant-centres (Sagarin and Gaines 2002) or “hot spots” (Brown et al. 1995) would presumably shift through time as conditions change. For example, as habitat is lost or degraded across a species geographic range, presumably the centres of relative abundance could change and the distribution of demographic processes such as

immigration would also change dynamically. The specific location of an abundant-centre of a historical distribution would probably not be the same location as an abundant-centre of the extant or final range, nor for intermediate ranges during the collapse. As environmental conditions change and extrinsic forces of extinction are experienced by central populations, other populations will surely begin to have higher relative abundances and accompanying variations in demographic characteristics such as population variability and immigration/emigration. In essence, the demographic hypothesis, as postulated (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b), was not dynamic enough to truly represent the changes that would be expected of abundant-centres and associated demographic patterns over time. Ultimately, its shortcoming was that it was unrealistically based strictly on the demographic characteristics of the historical populations (Channell and Lomolino 2000b). If the potential for dynamic abundant-centres is acknowledged, then traditional demographic processes based on the abundant-centre distribution (Grinnell 1922, Andrewartha and Birch 1954, Udvardy 1969, Hengeveld and Haeck 1982, Rapoport 1982, Brown and Gibson 1983, Brown 1984, Gaston 1990, Hengeveld 1990, Maurer 1994, Brown et al. 1995, Lawton 1995, Hochberg and Ives 1999, Sagarin and Gaines 2002) and island biogeography theory (MacArthur and Wilson 1967, Goel and Richter-Dyn 1974, Brown and Kodric-Brown 1977, Pimm et al. 1988, Tracy and George 1992) do not necessarily preclude persistence of some peripheral populations. That is, populations that were historically peripheral and may once have been characterized by low and variable abundances and immigration rates, will not necessarily have such characteristics subsequently as the environmental conditions and overall geographic range change. Historical demographic patterns should

not be assumed to dictate subsequent demographic patterns, especially when conditions have presumably changed significantly through time.

I also suggest that many demographic and contagion-like processes should be correlated and together contribute to disproportionate persistence of species in the peripheries. Susceptibility of populations to many types of extrinsic factors should often be correlated with demographic considerations such as population density, immigration, or distance from the nearest population. For example, newly introduced species that prove to be highly competitive with endemic species or inflict disease or other negative effects on endemic species should be expected to spread more successfully, and more rapidly, between habitats that are relatively continuously distributed. However, habitats towards the peripheries of species ranges tend to be more fragmented and heterogeneous (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b) and should therefore slow or even halt the spread of such factors. Equally, any extrinsic force of extinction that is carried by immigrants, such as contagious disease, should spread successfully and rapidly throughout central regions of a species range but more slowly among the relatively isolated populations near the peripheries. Furthermore, geographic segregation would also promote persistence of peripheral populations even in the case of anthropogenic habitat degradation, such as fragmentation. Habitat loss and fragmentation may be expected to have more impact on particular species in those areas where the species' habitats were historically continuous and relatively homogeneous, which again is more typical of central populations and less typical of smaller, more isolated patches of habitat near the peripheries of species ranges. Overall, remote populations should receive less immigration but at the same time should be more independent of the perturbations that

more central populations are exposed to. This is analogous to predictions made from metapopulation theory (Levins 1970, Hanski 1994, Hanski 1998): the overall probability of extinction for a metapopulation is reduced if it is distributed among several local populations whose dynamics are relatively independent of each other.

The black-footed ferret may be an excellent case in point. Its final, extant population near the western periphery of the species geographic range may not have suffered from the same degree of anthropogenic effects, such as habitat alteration and introduced diseases, specifically because of its demographic characteristics. The population occupied a small, remote area and therefore its habitat probably experienced minimal anthropogenic effects and the population rarely received immigrants that could have increased the prevalence of diseases (Anderson et al. 1986, Forrest et al. 1988). Clearly then, well established demographic processes should not be considered mutually exclusive from the contagion hypothesis for explanations regarding the apparent persistence of peripheral populations.

Another important consideration that is likely to contribute to the tendency for peripheral populations to represent the last remaining strongholds of species (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b) is the component of population diversity (Lesica and Allendorf 1995, Hughes et al. 1997, Myers 1997, Ceballos and Ehrlich 2002, Luck et al. 2003). Population diversity refers to all the variation inherent in distinct populations that comprise a species across its geographic range. Population diversity may be even more critical to comprehend and conserve than species richness (Ehrlich 1988, Hughes et al. 1997), given that populations contribute incrementally to ecosystems (Hughes et al. 1997, Luck et al. 2003) and that some populations will presumably be more viable than

others through periods of environmental change. For a given species, a large number and diversity of populations should reduce the odds that none of the populations are able to cope with a particular disturbance or environmental change. Accordingly, I theorize that there is considerable justification to predict persistence of peripheral populations because they increase intraspecific diversity, thereby increasing the likelihood that at least one population will possess some traits that assist in contending with a certain perturbation.

Early biogeographers recognized that species traits (e.g., body size and allometry) vary predictably along climate gradients (e.g., Bergmann's rule; Mayr 1963). Peripheral populations are usually exposed to markedly different environmental conditions, relative to more central populations (Hoffman and Blows 1994, Lesica and Allendorf 1995). Natural selection should therefore favor individuals that possess characteristics that are suited specifically to those (peripheral) locales. As a result, peripheral populations should contribute disproportionately more to the overall diversity of a species than more central populations. Moreover, populations in the peripheries also tend to be distributed among fragmented and geographically isolated habitats (Mayr 1963, Levin 1970, Hengeveld and Haack 1982, Brown 1984, Gaston 1990, Lawton 1993, Brown et al. 1995). Geographic isolation of peripheral populations, beyond maximum dispersal distances of a species, should cause populations to evolve in genetic isolation. Genetic isolation should enhance founder effects and genetic drift (Lesica and Allendorf 1995), which should further contribute to overall genetic heterozygosity of the species. As a result, populations near the peripheries presumably contribute disproportionately more to the total population diversity of a species than do more central populations (Gaston 1990, Ridley 1993, Hoffman and Blows 1994). The genetic

diversity within any particular peripheral population may itself be low (Lesica and Allendorf 1995); however, cumulatively the genetic diversity across many peripheral populations should be high. During periods of future environmental change or perturbation, species with high diversity of populations should be more likely to have at least one population persist than species that do not have high population diversity (Lomolino and Channell 1995). Hence I conclude that population diversity should be considered an important benefit of peripheral populations and that population diversity in the peripheries is likely to favor persistence of species in peripheral areas.

Broad-scale conservation of peripheral populations will undoubtedly demand substantially more resources than focused conservation of strictly central populations. Furthermore, any single peripheral population will not necessarily persist. Dependent on the particular cause of population declines and extinctions, which is not usually realized until the collapse of the species range is well underway, it is impossible to predict which peripheral populations are likely to persist and which may collapse. What is clear, however, is that there are many reasons to predict persistence of peripheral populations. Peripheral populations should not be discounted: the very characteristics that make them peripheral may in fact be their saving grace.

Summary

I reviewed general patterns of distribution and abundance, their relevance to peripheral populations, and quantitative models of peripherality. I presented and evaluated a new weighted-distance model of peripherality that is logically consistent with the concept of peripherality. The weighted-distance model incorporates information about both: (i) proximity to the range limits, where environmental conditions would

usually be most different from the centre and nearest to those extremes that delimit population viability; and (ii) distance from the centre, as another equally important index of similarity for spatially autocorrelated factors such as environmental conditions, as well as population connectivity or genetic relatedness. The resultant estimate of peripherality is a continuous variable that can be ranked or categorized as necessary for statistical analyses of biogeographical patterns. To evaluate the potential importance of peripheral populations in biodiversity conservation, the apparent biogeographical pattern of persistence of peripheral populations should be reassessed according to the weighted-distance model of peripherality.

Regardless of shortcomings of previous models of peripherality, I propose that persistence of peripheral populations is expected due to both population diversity and geographic segregation from spatially autocorrelated perturbations. This hypothesis provides a complementary explanation for the biogeographical patterns that were recently reported by other authors (Lomolino and Channell 1995, Lomolino and Channell 1998, Channell and Lomolino 2000a, Channell and Lomolino 2000b). Populations near the peripheries should not be discounted, nor should conservation efforts in the peripheries be discouraged, because peripheral populations are likely to facilitate the persistence of species during periods of increasing anthropogenic perturbations, such as habitat loss and fragmentation or climate change. Consequently, I suggest that peripheral populations have a more important role for biodiversity conservation than previously articulated.

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**APPENDIX B. CLIMATOLOGICAL MAPS OF THE GEOGRAPHIC RANGES
OF BLACK-TAILED PRAIRIE DOGS (*CYNOMYS LUDOVICIANUS*) AND
ORD'S KANGAROO RATS (*DIPODOMYS ORDII*)**

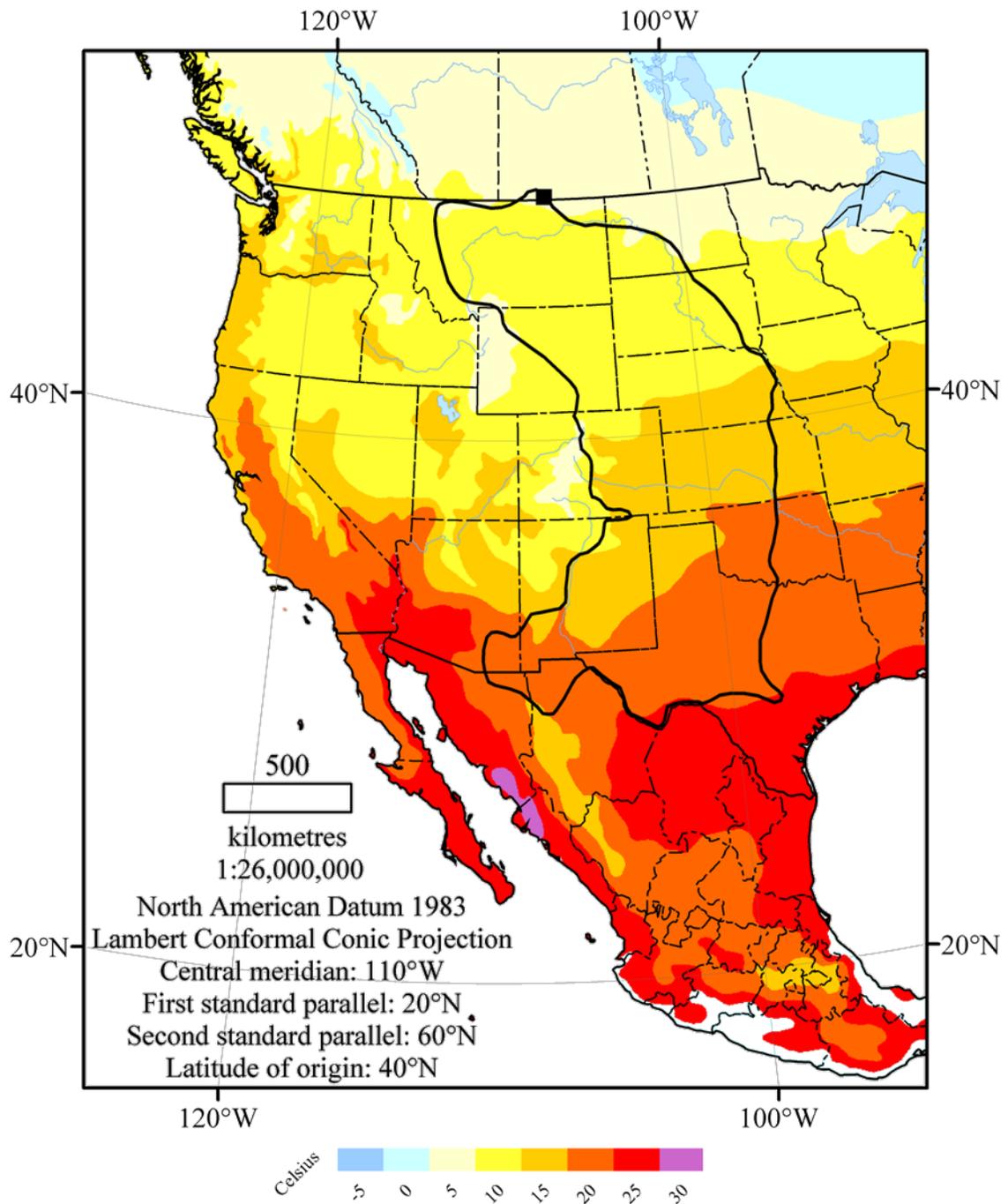


Figure B.1 Map of mean annual temperature for southwestern North America overlaid with the geographic distribution of black-tailed prairie dogs (*Cynomys ludovicianus*). The location of my prairie dog study area is indicated by a black square symbol. Temperature data were obtained from Environmental Systems Research Institute (1999; “World Temperature Zones” [map] <http://www.geographynetwork.com/>).

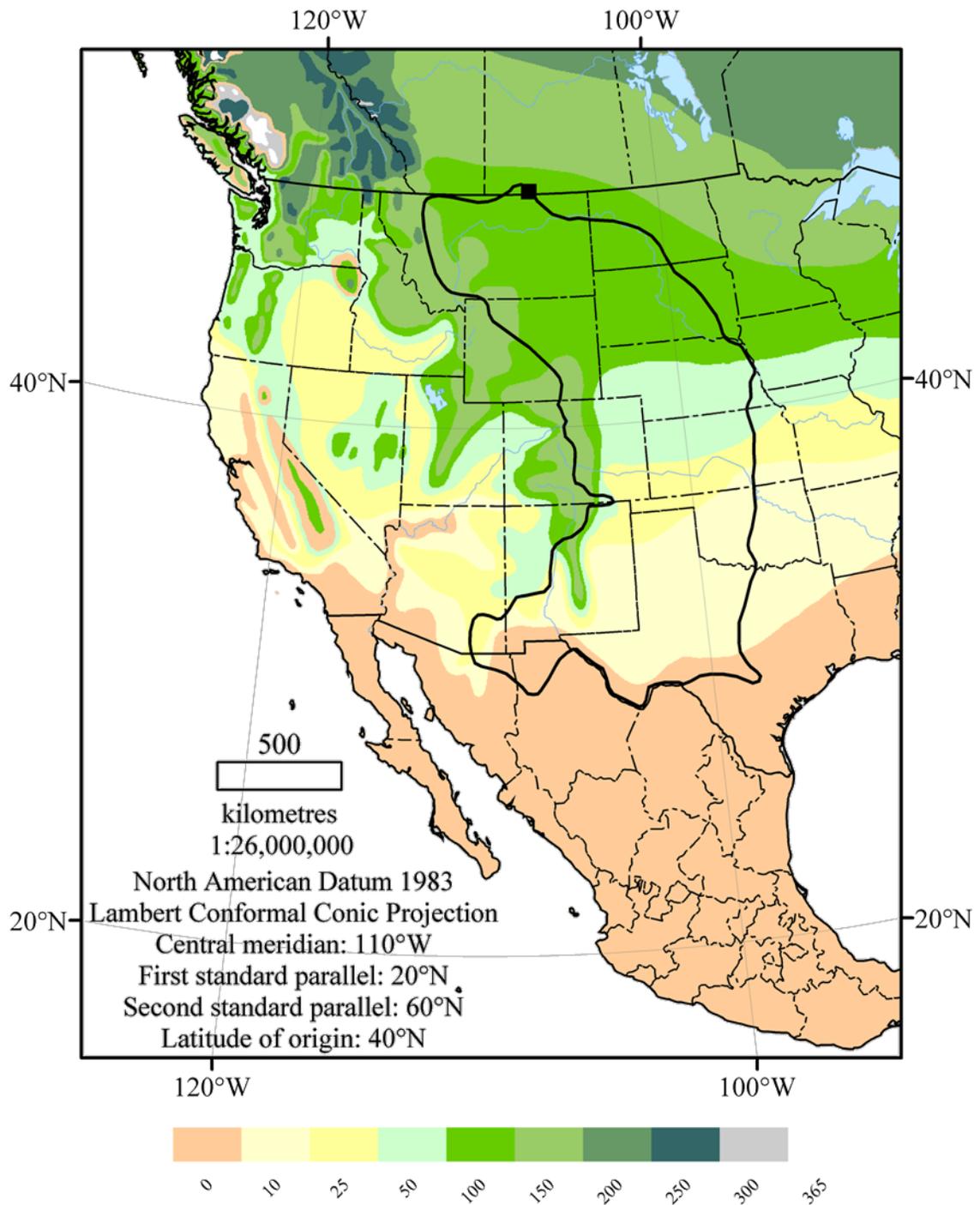


Figure B.2 Map of mean annual number of days with snow for southwestern North America overlaid with the geographic distribution of black-tailed prairie dogs (*Cynomys ludovicianus*). The location of my prairie dog study area is indicated by a black square symbol. Snow data were obtained from Environmental Systems Research Institute (1999; “World Snow Cover” [map] <http://www.geographynetwork.com/>).

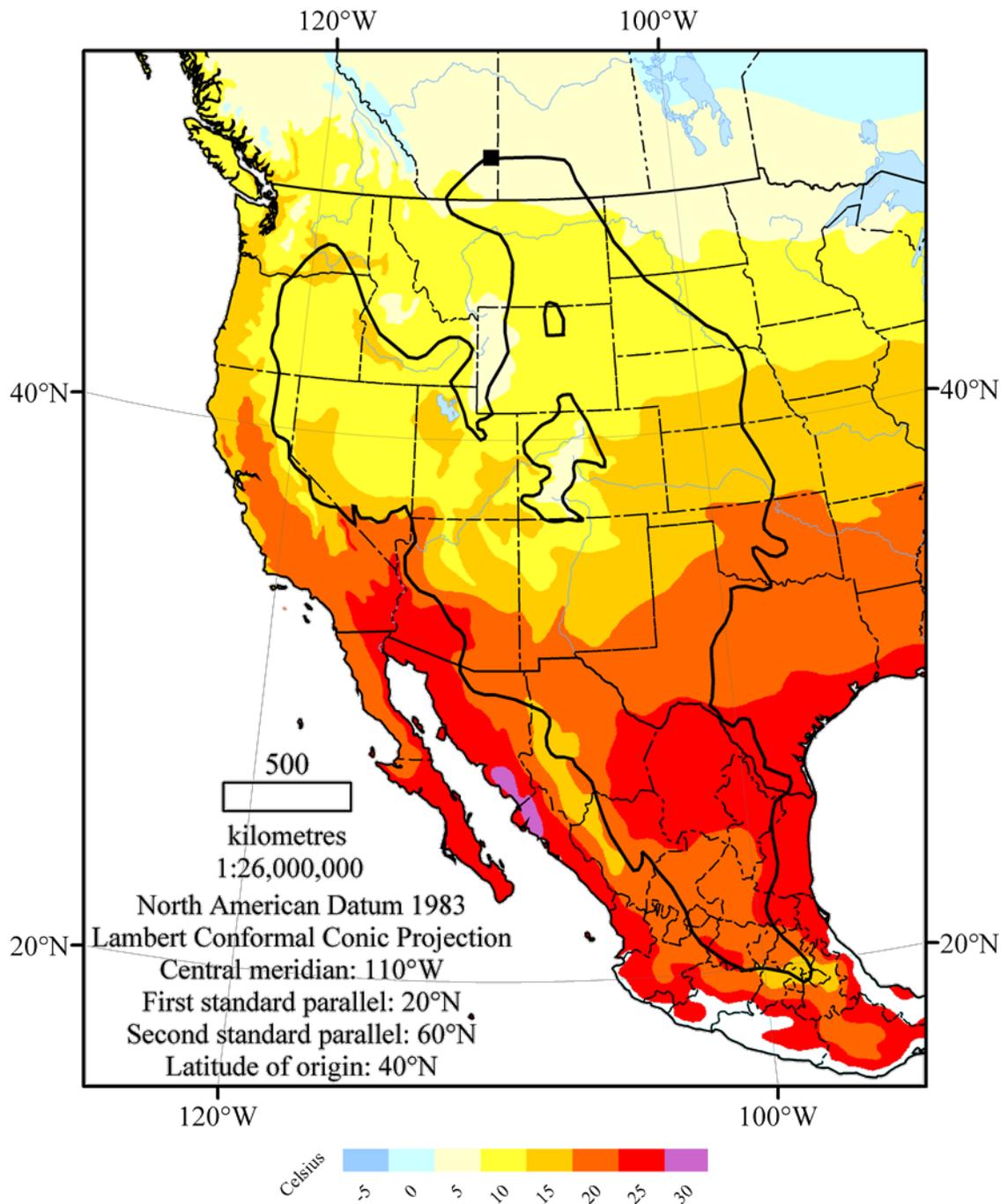


Figure B.3 Map of mean annual temperature for southwestern North America overlaid with the geographic distribution of Ord's kangaroo rats (*Dipodomys ordii*). The location of my kangaroo rat study area is indicated by a black square symbol. Temperature data were obtained from Environmental Systems Research Institute (1999; "World Temperature Zones" [map] <http://www.geographynetwork.com/>).

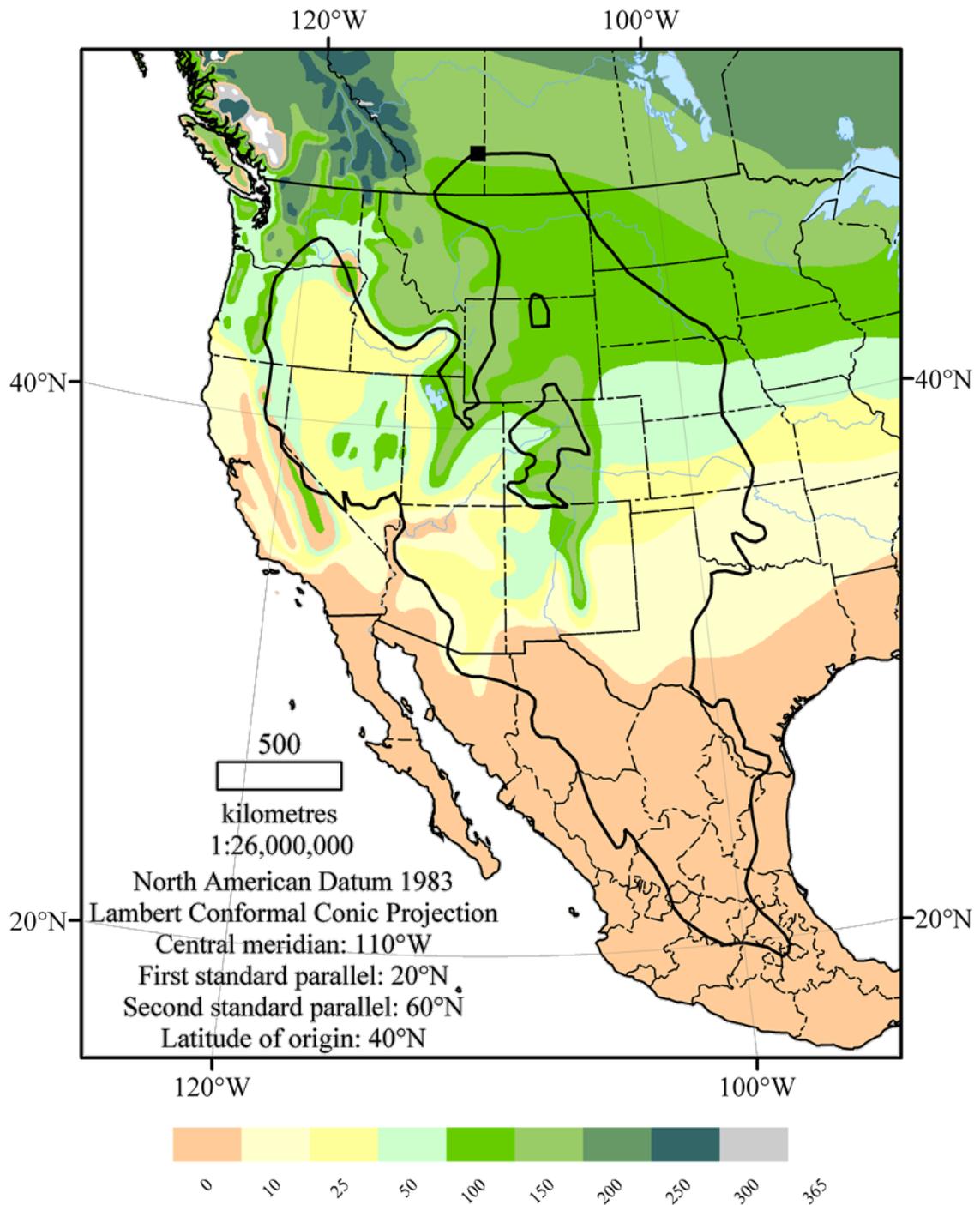


Figure B.4 Map of mean annual number of days with snow for southwestern North America overlaid with the geographic distribution of Ord's kangaroo rats (*Dipodomys ordii*). The location of my kangaroo rat study area is indicated by a black square symbol. Snow data were obtained from Environmental Systems Research Institute (1999; "World Snow Cover" [map] <http://www.geographynetwork.com/>).