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Spatial Patterns and Effects of Bot Fly (*Cuterebra polita*) Parasitism in
Ord's kangaroo rat (*Dipodomys ordii*)

by

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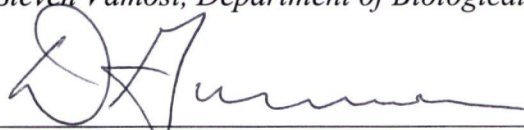
The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Spatial Patterns and Effects of Bot Fly (*Cuterebra polita*) Parasitism in Ord's kangaroo rat (*Dipodomys ordii*)" submitted by Sandra Elaine Robertson in partial fulfilment of the requirements of the degree of Master of Science.



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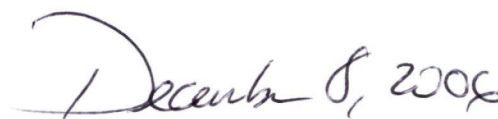
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Abstract

I evaluated the influence of different habitat types and habitat connectivity on bot fly parasitism of Ord's kangaroo rat. Parasitism was not significantly associated with habitat connectivity. However, bot fly prevalence differed significantly among habitat types. Mean prevalence was not significantly different between sand dune and road habitat, but was significantly lower in areas along the river valley. Bot fly larvae were found in 30% of kangaroo rats captured between July 12 and October 13, 2004.

Prevalence did not vary significantly with host age or sex. I found that bot fly parasitism was not significantly associated with the body condition, reproductive status, and survival of kangaroo rats. Bot fly parasitism was negatively correlated with an estimated measure of juvenile recruitment. The potential impact of parasitism on juvenile recruitment may have detrimental effects on the population growth of kangaroo rats.

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CHAPTER 1

GENERAL INTRODUCTION

A potential consequence of anthropogenic disturbance of wildlife habitat is an increase in the prevalence of parasitic diseases for wildlife (McCallum and Dobson 1995, Schrag and Wiener 1995, Daszak et al. 2000, Patz et al. 2000). For instance, the creation of a reservoir in Brazil resulted in significantly greater tick infestations in the endangered marsh deer (*Blastocerus dichotomus*; Szabo et al. 2003), and logging in Uganda caused greater parasitic infections in redbellied guenons (*Cercopithecus ascanius*; Gillespie et al. 2005). One of the most widespread forms of habitat disturbance is the construction and maintenance of roads (Forman and Alexander 1998, Trombulak and Frissel 2000). In addition to the direct disturbance, roads may contribute to an increase in parasitism by facilitating the movement of parasites, vectors, and hosts, but also by creating favorable conditions for the parasite, as well as the host (Patz et al. 2000, Urban 2005).

The Ord's kangaroo rat (Heteromyidae: *Dipodomys ordii* Woodhouse, 1853) is an example of a species that may be experiencing high rates of parasitism from a novel parasite as a result of habitat disturbance caused by the development of roads. Canadian Ord's kangaroo rats represent the northernmost kangaroo rat population, and this population is the only one known to be parasitized by bot fly larvae. From a study in southeastern Alberta, Gummer et al. (1997) provides the only report of bot fly, *Cuterebra polita* Coquillett, 1898 (Diptera: Oestridae), parasitism in Ord's kangaroo rat.

Observations from kangaroo rat surveys in Alberta between 1999 and 2002 suggest that bot fly parasitism may be more prevalent in kangaroo rats occupying roads compared to natural habitat (Figure 1.1; D. L. Gummer pers. comm.).

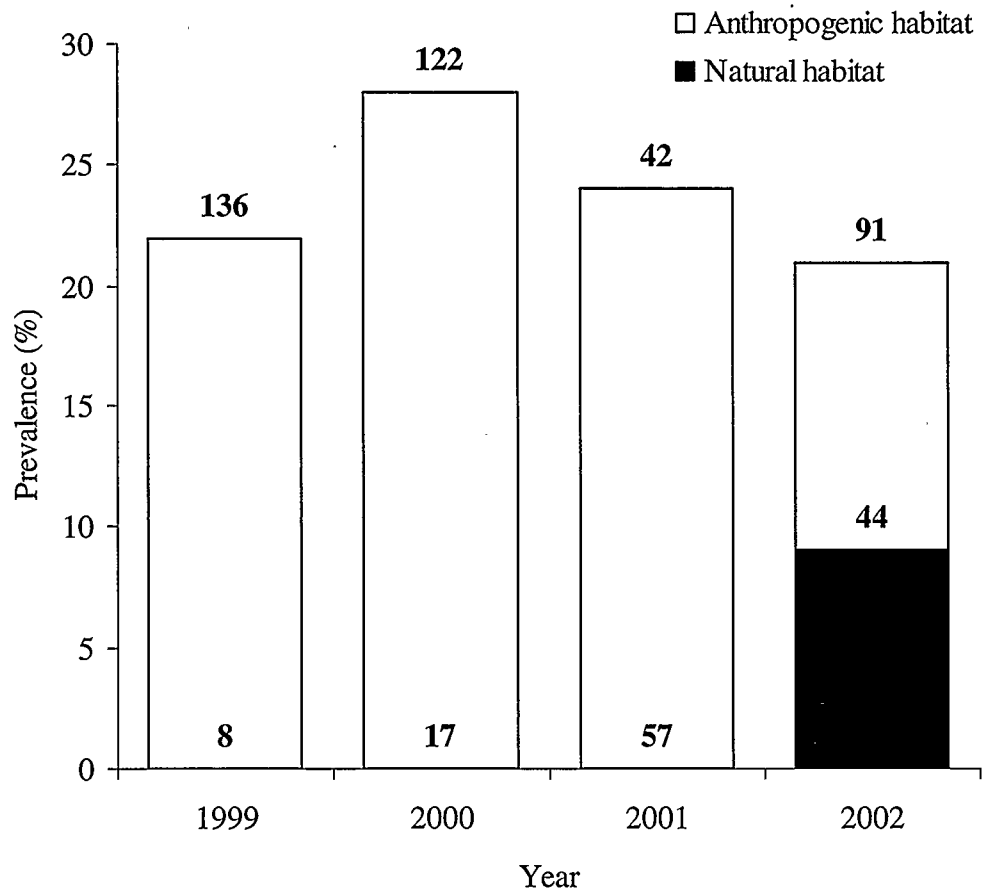


Figure 1.1. Rates of bot fly parasitism for the Ord's kangaroo rat population in Alberta. The bold numbers are the number of individuals captured during the bot fly season in road habitats (top numbers) and natural habitats (bottom numbers). Parasitism rates were zero in natural habitats for all years except 2002. From Gummer unpubl. data.

Kangaroo rats are fossorial (living underground) and use saltatory (leaping) locomotion; therefore, they require areas with sandy soils and sparse vegetation, particularly sand dunes, arid grasslands, and open scrubland environments (Maxwell and Brown 1968, Armstrong 1979). Natural kangaroo rat habitat, particularly active sand dunes, is rapidly disappearing (Muhs and Wolfe 1999; COSEWIC 2006). The decrease in sand dunes may be due to long-term changes in climate, fire regimes, and ungulate grazing (Muhs and Wolfe 1999). Nonetheless, natural habitat is present and available to kangaroo rats, but it is rare and isolated. The development of trails, roads, and fireguards in sandy areas has created alternative 'anthropogenic' habitat, which kangaroo rats also occupy. The anthropogenic habitat provides the open, sandy habitats that kangaroo rats require, and kangaroo rats have become relatively abundant in this habitat type, even though the quality of this habitat is presumed to be much lower (COSEWIC 2006). Incidentally, kangaroo rats are recognized as endangered in Alberta under the Alberta Wildlife Act, as well as in Canada by the Committee On the Status of Endangered Wildlife In Canada (COSEWIC 2006). Limited habitat and the decline of natural habitat contribute to this designation (COSEWIC 2006).

Bot fly parasitism has never been documented in southern Ord's kangaroo rat populations or for any other *Dipodomys* species (Gummer et al. 1997). Further, in the entire Heteromyidae family, only two species have been reported to be infected with bot fly parasites: the Mexican spiny pocket mice (*Liomys irroratus*; Parker and Chaney 1979) and hispid pocket mice (*Perognathus hispidus*; Goertz 1966). Since this parasitic association appears to occur in the Canadian kangaroo rat population only, I consider the kangaroo rat to be a relatively novel and atypical host for *C. polita*.

Cuterebra polita is reported to be a natural parasite of the northern pocket gopher (*Thomomys talpoides*; Richens 1965, Capelle 1970, Graham and Capelle 1970, Catts 1982, Sabrosky 1986), a species whose range overlaps with the Ord's kangaroo rat in Alberta (Smith 1993). Bot flies (also known as warble flies or bots) of the genus *Cuterebra* are considered host-specific but occasionally parasitize secondary or atypical hosts (Catts 1982). The receptiveness of atypical hosts to bot fly infection does not imply suitability, and such hosts often suffer detrimental effects (Catts 1982).

Adult female *Cuterebra* do not oviposit on their host; instead, they deposit eggs on vegetation, often near burrow entrances (Catts 1982). Interestingly, *C. polita* is the only *Cuterebra* species that has been observed to deposit eggs inside the burrow of its host (Capelle 1970, Catts 1982). Infection occurs when the host animal moves through its burrow; the body heat from the host stimulates the eggs to hatch and the larvae to adhere to the host. The larvae then enter the host's body via moist openings (e.g., mouth, nostrils, or eyes; Catts 1982). The first instar larva migrates through the host's body and emerges through the tissue, creating a breathing hole (known as a warble pore), then it molts to its second stage (Catts 1982). The larva remains in this subcutaneous position and feeds until it molts into the final, third instar stage (Catts 1982). Third instar larvae are approximately 20 mm long and 1 g in mass (Capelle 1970, Gummer et al. 1997). The duration of *C. polita* larval development in the host can last for 20 - 42 days, after which the larva emerges from the host and burrows into the soil to pupate until the following spring (Capelle 1970, Catts 1982).

There have been extensive studies on the effects of bot fly infection on the host: *Peromyscus maniculatus* (Sealander 1961, Hunter et al. 1972); *Peromyscus leucopus*

(Wecker 1962, Payne and Cosgrove 1965, Dunaway et al. 1967, Miller and Getz 1969, Hensley 1976, Timm and Cook 1979, Munger and Karasov 1991, Burns et al. 2005); *Microtus pennsylvanicus* (Clough 1965, Iverson and Turner 1968, Getz 1970); *Tamias striatus* (Bennett 1973, Jaffe et al. 2005); and *M. townsendii* (Boonstra et al. 1980).

Studies on the effects of *Cuterebra* infection in atypical hosts have mainly taken place in a laboratory setting and studies in the field are limited.

In general, these studies find that there are few detrimental effects of parasites on typical hosts. Whereas, detrimental effects may occur in atypical hosts. The findings of individual studies are discussed in more detail in subsequent chapters.

Research Objectives

My thesis examines the relationship between the Ord's kangaroo rat and the bot fly, *C. polita*. I examine the potential influence of anthropogenic habitat on bot fly parasitism rates, as well as the effects of bot fly parasitism on the body condition, reproduction, and survival of kangaroo rats.

Thesis Outline

In Chapter 2, I report the temporal pattern of parasitism, prevalence and intensity of parasitism, and warble location. In Chapter 3, I present the results on the influence of habitat type and connectivity on parasitism, and the influence of kangaroo rat density on prevalence. In Chapter 4, I present the results regarding the effects of bot fly parasitism on kangaroo rat body condition, reproduction, and survival. In Chapter 5, I discuss the efficacy of various methods for surveying adult bot flies; I report methods, results, and recommendations regarding daytime surveys for adult bot flies in the field, and the outcome of rearing bot fly larvae. Finally, in Chapter 6, I include a summary of my

research, a synthesis of results, recommendations for further research, and management implications.

RESEARCH METHODS

Study Area

I conducted this study in the Suffield National Wildlife Area (SNWA) in Canadian Forces Base (CFB) Suffield in southeastern Alberta (Figure 1.2). No military training activities are permitted in the SNWA, but there is extensive oil and gas activity and limited livestock grazing. The northern portion of the SNWA contains much of the Middle Sand Hills, a complex of stabilized, partially stabilized, and active sand dunes (Muhs and Wolfe 1999, Reynolds et al. 1999). The southern portion of the SNWA is composed of rolling hills and flat to undulating plains (Dale et al. 1999). The summers tend to be very hot and dry, daytime temperatures can reach 30-35°C, and the average summer rainfall is 156 mm (Adams et al. 1997). The winters in this area are cold and experience little snowfall. The average winter temperature is -7.2°C and can reach as low as -40°C (Adams et al. 1997).

My study area lies within the dry mixed-grass prairie subregion of Alberta. The dominant cover includes species such as needle and thread grass (*Stipa comata*), speargrass (*Aciphylla squarrosa*), northern wheatgrass (*Agropyron dasytachyum*), and blue grama grass (*Bouteloua gracilis*; Adams et al. 1997). Woody vegetation is sparsely dispersed throughout the

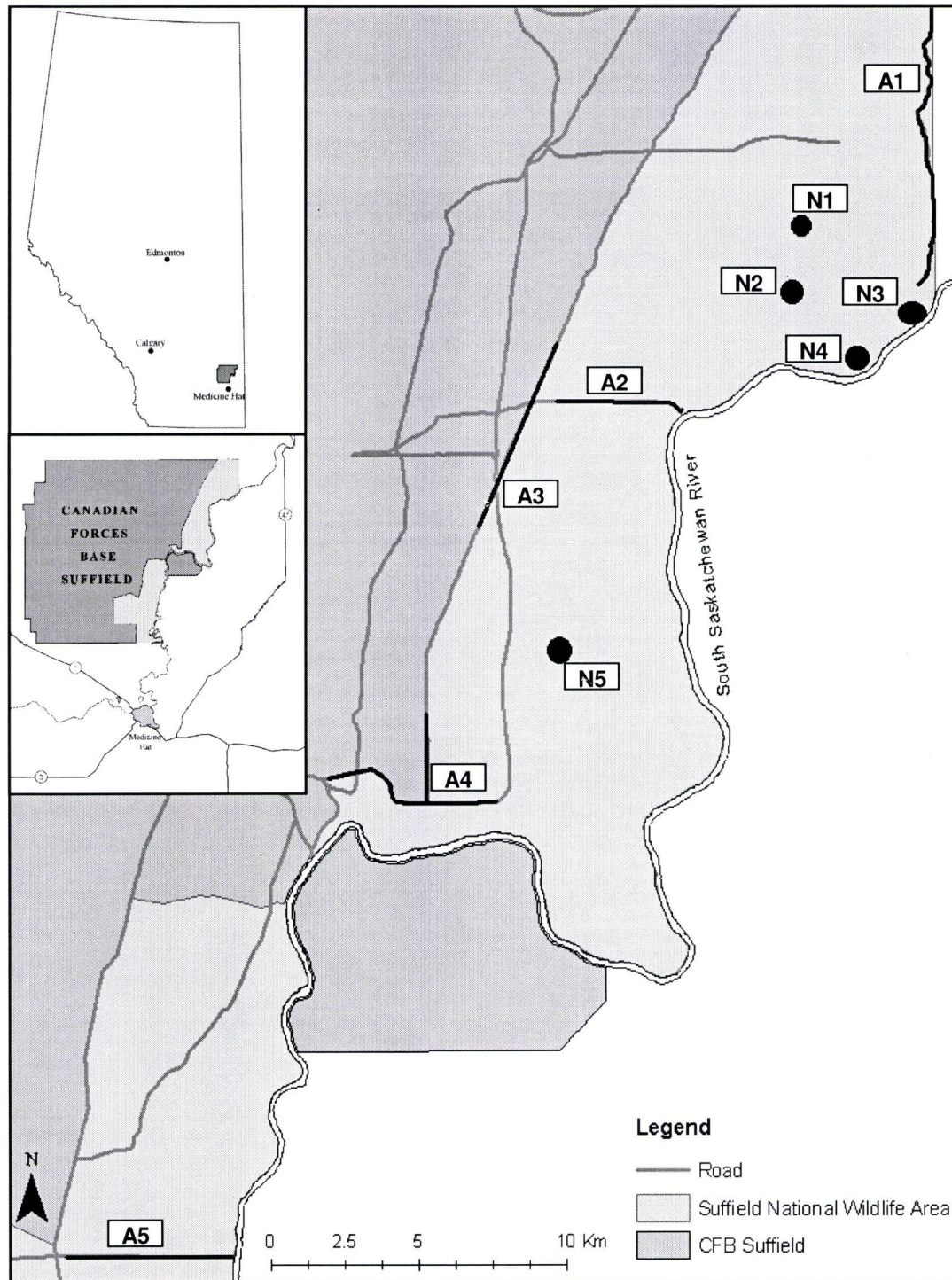


Figure 1.2. Ord's kangaroo rat study sites in the Suffield National Wildlife Area in Canadian Forces Base Suffield. The road segments in bold are the anthropogenic study sites (denoted as 'A') and the circles are the natural study sites (denoted as 'N').

landscape. Common shrubs include sagebrush (*Artemisia cana*), wild rose (*Rosa woodsii*), and choke cherry (*Prunus virginiana*; Adams et al. 1997). Common plants associated with sand dune areas include lance-leaved psoralea (*Psoralea lanceolata*), Indian rice grass (*Oryzopsis hymenoides*), and prairie sand-reed grass (*Calamovilfa longifolia*; Adams et al. 1997). Exotic vegetation, such as Russian thistle (*Salsola kali*), crested wheat grass (*Agropyron cristatum*), and leafy spurge (*Euphorbia esula*) exists along roads and trails (Adams et al. 1997).

I studied kangaroo rats at five natural and five anthropogenic (i.e., road) sites (Figure 1.2). The natural sites include three active sand dune habitats and two sandy exposures along the South Saskatchewan River valley in the northern portion of the SNWA. The anthropogenic sites consist of sandy, loose-surfaced roadways used as access routes and firebreaks, however, traffic volume is very low.

General Field Techniques

I conducted mark-recapture surveys of Ord's kangaroo rats using two techniques. Surveys along roads involved driving a vehicle slowly (ca. 30 km/hr) with the headlights on, and two persons searching with spotlights (1 million candlepower, model 800-2500-0, Brinkmann Corporation, Dallas, Texas) from the side windows (Kaufman and Kaufman 1982). When a kangaroo rat was detected, one person kept the spotlight on the animal while the other pursued on foot and captured it by hand (Gummer et al. 1997). It was not possible to survey natural areas by vehicle, consequently surveys were conducted on foot with bright flashlights (6-D cell Maglite, Mag Instrument, Inc., Ontario, California) to locate kangaroo rats. When an animal was spotted, it was pursued and captured by hand.

I marked each kangaroo rat with a uniquely coded microchip (Passive Integrated Transponder; Avid Canada, Calgary, Alberta) and uniquely numbered ear tag. Microchips were implanted subcutaneously on the hip using a sterile hypodermic needle. Ear tags were attached to one ear of the animal. At each capture, I recorded the date, time, habitat type, and location of capture, recorded in Universal Transverse Mercator coordinates (UTM zone 12, World Geodetic System 1984 datum) with a global positioning system (GPS; Garmin 12CX, Olathe, Kansas). As well, I recorded the microchip code, ear tag number, mass (± 1 g, spring scale; Pesola AG, Baar, Switzerland), tail length (± 1 mm), sex, age class, reproductive condition, and description of parasites. I categorized individuals into one of two age groups: juvenile (young of the year) or adult (at least one year old), based on body mass, tail length, and pelage. I based the reproductive condition on external physical characteristics. The reproductive condition of females was recognized by enlargement of the vulva (estrous); the presence of a mate plug (recent mating); abdominal swelling (pregnant); red, swollen, worn mammae (lactating); pale, bare, worn mammae (post-lactating); and no external sign (non-reproductive; Day et al. 1956, Smith et al. 1978, Gummer 1997a). I considered males reproductively active if their testes were descended from the abdominal cavity (Garrison and Best 1990, Gummer 1997a).

I thoroughly examined each captured kangaroo rat for the presence of parasites. *Cuterebra* parasitism is obvious because larvae are located just under the skin, and the posterior end of the bot is visible through the warble pore. If an individual was parasitized with *Cuterebra* larvae, I recorded the number of larvae, location of each larva on the host's body, approximate developmental stage, and condition (e.g., purulence,

septic, odour). The larval development stage was determined based on the color and size of larvae. First and second instar larva are creamy white and <10 mm in length, late second instar and early third instar larvae are darker in color and approximately 15 mm in length, and mature third instar larva are dark brown and approximately 20 mm in length (Sillman 1955, Capelle 1970). I also recorded the presence of other parasites, such as fleas, ticks, and mites.

CHAPTER 2

PREVALENCE AND INTENSITY OF BOT FLY PARASITISM IN ORD'S KANGAROO RAT

INTRODUCTION

Cuterebra evolved with certain major lines of New World rodents and are known to commonly parasitize small mammals such as tree squirrels, chipmunks, pocket gophers, mice, woodrats, and voles. Bot fly parasitism has not been associated with kangaroo rats (Catts 1982, Sabrosky 1986), yet Gummer et al. (1997) observed *Cuterebra* parasitism in Ord's kangaroo rats in Alberta.

Rates of parasitism and parasite burden are reported for several natural host species of *Cuterebra*. Infection occurs when a susceptible host comes into contact with bot fly larva. It has been hypothesized that the more active gender (typically males) and age group (typically adults) should suffer higher parasitism rates (Xia and Millar 1990). However, the results are contradictory in the literature. Several authors report higher parasitism rates in males compared to females (Sealander 1961, Goertz 1966, Iverson and Turner 1968, Hensley 1976, Xia and Millar 1990, Smith and Edge 1996, Wilson et al. 1997), whereas no difference between genders is also frequently reported (Test and Test 1943, Wecker 1962, Dunaway et al. 1967, Miller and Getz 1969, Getz 1970, Hunter et al. 1971, Gingrich and Barrett 1976, Smith 1977a, Timm and Cook 1979, Boonstra et al. 1980, Clark and Kaufmann 1990, Kollars 1995, Gummer et al. 1997, Wilson et al. 1997, Adler et al. 2003, Burns et al. 2005, Jaffe et al. 2005). Similarly, parasitism rates have been observed to be higher in adults (Scott and Snead 1940, Miller and Getz 1969, Getz 1970, Hunter et al. 1971, Smith 1977a, Timm and Cook 1979, Xia and Millar 1990, Jaffe

et al. 2005; *P. leucopus*, *Tamias striatus*), yet there are several studies where no difference between age groups is found (Wecker 1962, Layne 1963, Baird 1979, Brigada et al. 1992, Gummer et al. 1997, Wilson et al. 1997, Adler et al. 2003, Burns et al. 2005, Jaffe et al. 2005; *P. maniculatus*).

Bot fly larvae migrate through the body of an infected host to a subcutaneous location, where they create a breathing hole (warble pore). In native hosts, this warble pore is typically located in a specific location on the host's body, considered to be an indicator of a well-adapted host-parasite relationship (Catts 1982, Zuleta and Vignau 1990). For instance, the warble pore of *C. fontinella* in white-footed mice (*P. leucopus*) is typically located in the inguinal (i.e., groin) region (Wecker 1962, Payne and Cosgrove 1965, Goertz 1966, Dunaway et al. 1967, Miller and Getz 1969, Barko 2003). However, the location of the warble pore in atypical hosts is often less specific, which can be damaging to the host (Catts 1965, Baird 1972, Catts 1982). Furthermore, in atypical hosts the warble pore is often less defined and may experience secondary infections. As well, empty warble pores are often purulent and slow to heal (Sillman 1959, Catts 1965, Baird 1971, Smith 1977a, Boonstra et al. 1980, Catts 1982). Therefore, it is important to report the location of the larvae on the host's body and the warble pore condition.

The purpose of this chapter is to report the temporal pattern of parasitism, prevalence and intensity of parasitism with respect to sex and age, and warble location.

METHODS

I conducted mark-recapture surveys of kangaroo rats between May and October 2004. Only kangaroo rats captured during the bot fly season, defined as the period

between the first and the last day that bot fly parasitism was observed in kangaroo rats, were included in the analysis. All other kangaroo rats captured before or after the bot fly season were disregarded. I considered a kangaroo rat to be parasitized if it was observed to have any indication of bot fly parasitism (i.e. larvae present, empty warble pore, or conspicuous scar) at any point during the bot fly season. I calculated two measures of parasitism: 1) prevalence—the total number of parasitized individuals divided by the total number of individuals examined; and 2) intensity—the number of parasites observed per parasitized individual at one time (*sensu* Margolis et al. 1982). It was not always possible to know the total number of larvae parasitizing an animal because an infected individual could have first instar larvae that were not yet visible. Therefore, the minimum intensity for each individual was reported.

I used Chi-square analysis to assess differences in prevalence between age groups and sex. I used a factorial analysis of variance (ANOVA) to examine the differences in mean intensity between age groups and sex. When a lack of normality or heteroscedascity was encountered, data were appropriately transformed.

Statistical analyses were performed using SYSTAT 11 (Systat Software Inc., Point Richmond, California). Where appropriate, I used a Levene's test to test for homoscedasiticy, one-sample Kolmogorov-Smirnov test with Lilliefors distribution to test for normality of residuals, and Shapiro-Wilks W test to test for normality. Data are presented as means $\pm$ standard error. I considered alpha levels of 0.05 to be statistically significant.

RESULTS

Temporal Pattern of Bot Fly Parasitism

I captured and examined 707 individual kangaroo rats from May 14, 2004 to October 21, 2004. I observed kangaroo rats parasitized by bot fly larvae for an approximate three-month period: the first observation occurred on July 12, 2004, and the last parasitized kangaroo rat was seen on October 13, 2004 (Figure 2.1). During the bot fly season, I conducted surveys on 86 nights and I captured 570 individual kangaroo rats.

Prevalence of Bot Fly Parasitism

I observed bot fly larvae in 172 (30.2%) of the 570 kangaroo rats captured during the bot fly season. Prevalence was not significantly different between males ($83/268 = 31.0\%$) and females ($81/273 = 29.7\%$; $\chi^2 = 0.11$, $df = 1$, $P = 0.74$). Fewer juveniles ($41/162 = 25.3\%$) were parasitized than adults ($123/379 = 32.5\%$), but the difference was not significant ($\chi^2 = 2.74$, $df = 1$, $P = 0.10$).

Intensity of Bot Fly Parasitism

Mean intensity of bot fly parasitism was 1.8 ± 0.08 ($n = 172$); the maximum intensity was 7. The majority of individuals appeared to harbour only one or two bots (Figure 2.2). The intensity data did not meet the assumption of normality, even after transformation. However, an ANOVA was used because it is robust to lack of normality (Zar 1984: 170), and the data satisfied the assumption of homogeneity of variances. The intensity of parasites did not differ significantly between males and females

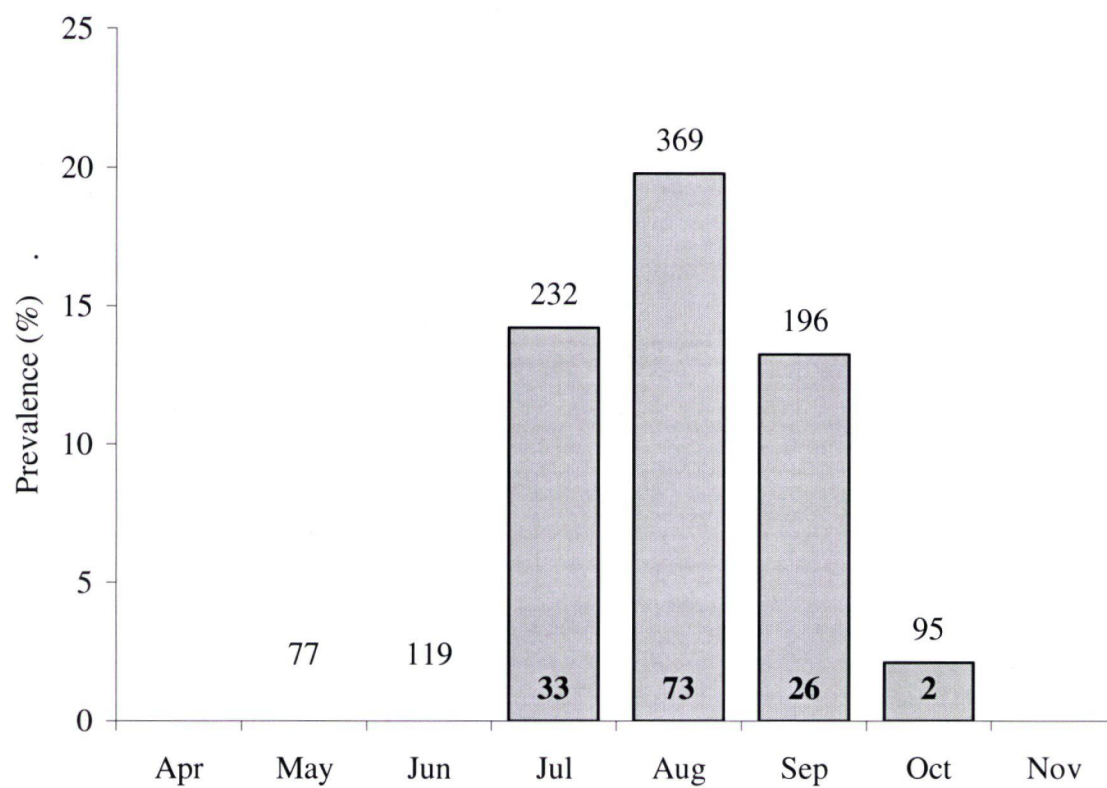


Figure 2.1. The percentage of Ord's kangaroo rats parasitized with *Cuterebra* larva during each month surveyed in southeastern Alberta in 2004; surveys were not conducted before May or after October. The number above each bar is the number of individuals captured in that month, and the number parasitized is shown in bold text.

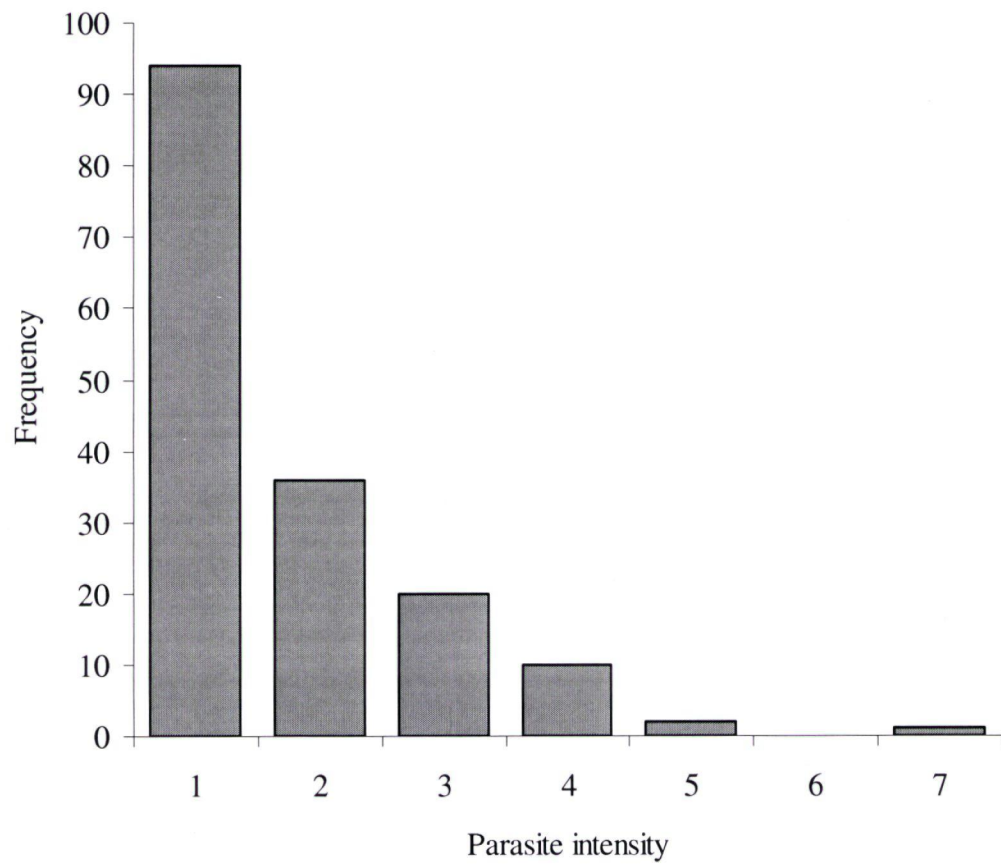


Figure 2.2. Frequency distribution of parasite intensity (number of bot fly larvae per individual) in Ord's kangaroo rats in southeastern Alberta in 2004.

($F = 0.173$, $df = 1$, 159 , $P = 0.68$); adults and juveniles (ANOVA, $F = 0.002$, $df = 1$, 159 , $P = 0.96$); nor was there a significant interaction with age and sex ($F = 0.195$, $df = 1$, 159 , $P = 0.66$; Table 2.1).

Warble Location

The location of warble development on the kangaroo rat's body was highly variable. Bot fly larvae established mainly in the lateral region (54.8%; hip and side) and ventral half (35.5%; abdomen, chest, and groin) of the kangaroo rat's body (Table 2.2). Less frequent locations were the back and face (Table 2.2).

DISCUSSION

The timing and duration of *C. polita* parasitism of Ord's kangaroo rats during this study, from July to October, was similar to previous studies of *Cuterebra* parasitism in the northern United States and southern Canada (*T. talpoides*, Jellison 1948; *P. leucopus*, Wecker 1962; *M. pennsylvanicus*, Clough 1965; *M. pennsylvanicus*, Iverson and Turner 1968; *P. leucopus*, Miller and Getz 1969; *M. pennsylvanicus*, Getz 1970; *P. maniculatus*, Hunter et al. 1972; *P. leucopus*, Timm and Cook 1979; *M. townsendii*, Boonstra et al. 1980; *P. leucopus*, Munger and Karasov 1991). However, studies in western Montana and central Washington have reported two infection periods, one during the spring and another in the late summer (Smith 1977a, Baird 1979).

Overall bot fly prevalence (30.2%) for kangaroo rats was similar to previous reports in kangaroo rats (34%; Gummer et al. 1997), as well as other small mammals (38%, Dalmat 1943; 32%, Sealander 1961; 19-33%, Dunaway et al. 1967; 32%, Getz 1970; 36%, Hunter et al. 1972; 31%, Hensley 1976). The results of *Cuterebra* prevalence

Table 2.1. Comparisons of parasite intensity in Ord's kangaroo rats by sex and age.

	Intensity of Bot Fly Parasitism							Mean	SE
	1	2	3	4	5	6	7		
Female	47	18	8	5	1	0	0	1.7	0.11
Male	47	18	12	5	1	0	1	1.8	0.13
Adult	73	24	16	7	2	0	1	1.7	0.10
Juvenile	21	12	4	3	0	0	0	1.7	0.15
Adult female	36	10	7	3	1	0	0	1.7	0.13
Adult male	37	14	9	4	1	0	1	1.8	0.15
Juvenile female	11	8	1	2	0	0	0	1.7	0.20
Juvenile male	10	4	3	1	0	0	0	1.7	0.23

Table 2.2. Development site of bot fly larvae on the body of Ord's kangaroo rat (n = 321 larvae).

Warble site	Number of larvae	Percent
Hip	120	37.4
Abdomen	101	31.5
Side	56	17.4
Back	28	8.9
Chest	7	2.2
Groin	6	1.9
Face or neck	3	1

between the sexes and age groups of animals were extremely variable in the literature, even within the same species. In this study, no difference existed in *Cuterebra* prevalence between adult and juvenile kangaroo rats, which agrees with studies by Wecker (1962), Layne (1963), Baird (1979), Brigada et al. (1992), Gummer et al. (1997), Wilson et al. (1997), Adler et al. (2003), Burns et al. (2005), and Jaffe et al. (2005; *P. maniculatus*). In contrast, prevalence was greater in adults compared to juveniles in studies by Scott and Snead (1940), Miller and Getz (1969), Getz (1970), Hunter et al. (1971), Smith (1977a), Timm and Cook (1979), Xia and Millar (1990), and Jaffe et al. (2005; *P. leucopus*, *Tamias striatus*); and prevalence was greater in juveniles compared to adults in studies by Hensley (1976), and Boonstra et al. (1980).

Like the majority of previous studies in small mammals, there was no difference in prevalence between male and female kangaroo rats, despite the fact that male kangaroo rats are more abundant and active (Garrison and Best 1990). This result has also been reported by Test and Test (1943), Wecker (1962), Dunaway et al. (1967), Miller and Getz (1969), Getz (1970), Hunter et al. (1971), Gingrich and Barrett (1976), Smith (1977a), Timm and Cook (1979), Boonstra et al. (1980), Clark and Kaufmann (1990), Kollars (1995), Gummer et al. (1997), Wilson et al. (1997), Adler et al. (2003), Burns et al. (2005), and Jaffe et al. (2005). However, Sealander (1961), Goertz (1966), Iverson and Turner (1968), Hensley (1976), Xia and Millar (1990), Smith and Edge (1996), and Wilson et al. (1997) have found prevalence to be higher in male animals. The lack of difference in prevalence between the sexes and age groups of kangaroo rats may be because female *C. polita* deposit their eggs inside the burrow (Capelle 1970). Therefore, each sex and age group should be equally as likely to come into contact with bot fly eggs,

regardless of their activity levels, since so much of a kangaroo rat's time is spent within the burrow (Gummer et al. 1997).

The average intensity of parasites per individual kangaroo rat (1.8) was only slightly lower than previous reports of 2.3 in kangaroo rats (Gummer et al. 1997) and 2.6 in the natural host, the northern pocket gopher (Richens 1965). Kangaroo rats have been observed to carry up to 11 parasites at one time (Gummer et al. 1997). However, in this study the greatest intensity observed was only 7.

Bot fly larvae were most commonly located in the hips, abdomen, and along the sides of the body, which was similar to that observed in previous reports of kangaroo rats (Gummer et al. 1997). Richens (1965) did not observe bots in the lateral region of northern pocket gophers infested with *C. polita*; the larvae were most commonly located in the ventroposterior region (i.e., inguinal, abdominal, and scrotal). However, Graham and Capelle (1970) observed *C. polita* larvae along the sides of the body of pocket gophers. Warble pores in the kangaroo rat appeared to be well developed in heavy-walled cysts; they were not soft and gelatinous as usually described for atypical hosts. Additionally, no secondary infections were observed, but the warble site often had considerable scab formation and purulence.

CHAPTER 3

THE INFLUENCE OF HABITAT TYPE AND CONNECTIVITY ON BOT FLY PARASITISM OF ORD'S KANGAROO RAT

INTRODUCTION

Previous studies that examined the relationship between bot flies (*Cuterebra* spp.) and their natural host indicate that habitat type plays a large role in the rate of parasitism. For instance, Hensley (1976) found higher bot fly parasitism rates in white-footed mice (*P. leucopus*) occupying woodlands compared to grasslands. Bennett (1972) observed higher bot fly parasitism rates in the eastern striped chipmunk (*Tamias striatus*) living in second-growth forests compared to mature coniferous forests. Wilson (1997) found parasitism rates to be significantly higher for white-throated woodrats (*Neotoma albigula*) on an arroyo (i.e., an intermittently dry creek) containing juniper, shrubs, and cacti compared to a more open hilltop habitat. Smith (1977a) and Bowman (2000) both reported that small mammals were more likely to be parasitized at riparian softwood stands rather than upland hardwood stands.

Habitat disturbance may also influence bot fly parasitism rates, although few studies have examined this. In general, small mammals occupying disturbed areas and edge habitat were shown to experience increased levels of *Cuterebra* parasitism compared to areas with little human disturbance. For example, a study on the impacts of clearcutting on small mammals found that deer mice (*P. maniculatus*) and creeping voles (*M. oregoni*) living in clearcuts suffered *Cuterebra* parasitism, while those in the forest did not (Cockle and Richardson 2003). In another study, Wolf and Batzli (2001) examined bot fly prevalence among edge habitat, forest habitat, and open areas, and

found that species occupying edge habitat experienced significantly greater parasitism rates than in the other habitat types.

The reasons for differential parasitism among different habitats are generally unknown, although microenvironment, availability of aggregation sites for adult flies, and the presence of appropriate habitat to deposit eggs may be contributing factors (Layne 1963, Goertz 1966, Dunaway et al. 1967, Getz 1970, Hensley 1976, Wolf and Batzli 2001). Capelle (1970) and Graham and Capelle (1970) suggest that the bot fly species, *C. polita*, that parasitize kangaroo rats use visual cues to locate the burrows of potential hosts. The typical host (i.e., northern pocket gopher) for *C. polita* creates mounds of bare soil during burrow construction and maintenance (Rogers et al. 2001). Therefore, I hypothesized that adult *C. polita* females cue in on open bare ground or disturbed soil to find the burrows of their typical host.

The Canadian population of the Ord's kangaroo rat is an atypical host for *Cuterebra*. Little is known about the factors influencing parasitism rates of kangaroo rats. Given the previous studies indicating the importance of habitat type and disturbance on bot fly parasitism, it is logical to expect that habitat disturbance may also play a significant role in the rate of bot fly parasitism in the Canadian kangaroo rat population.

Natural habitats of kangaroo rats in Alberta consist of sand dunes and sparsely vegetated areas along the South Saskatchewan River valley. These habitats are naturally dispersed and isolated throughout the landscape. Alternative habitats occupied by kangaroo rats consist of linear anthropogenic features, such as sandy roads, trails, or fireguards, which are frequently disturbed and highly connected. Additionally, kangaroo rats occupying these anthropogenic habitats tend to excavate conspicuous burrows along

the edges. Therefore, the high connectivity of anthropogenic habitat may facilitate movements by *C. polita*, which would be expected to increase the encounter rate with burrows of kangaroo rats. The combination of disturbance and connectivity of anthropogenic habitat, plus the sequential arrangement of conspicuous kangaroo rat burrows along roads, may predispose kangaroo rats occupying anthropogenic habitat to *C. polita* parasitism.

Research Objectives

The objective of this study was to determine if bot fly parasitism rates in kangaroo rats are related to habitat (i.e., disturbance and connectivity). Habitat disturbance (i.e., roads) may have produced conditions that attract bot flies, and the connectivity of anthropogenic habitat may facilitate bot fly movement, thereby increasing the bot fly's encounter rate with kangaroo rat burrows. I predicted that prevalence and intensity of bot fly parasitism will be significantly higher at road sites compared to natural sites. I also predicted that prevalence and intensity will be positively correlated with habitat connectivity; more connected habitats will have higher prevalence and intensity than isolated habitats.

METHODS

Measuring Connectivity of Anthropogenic Sites

In this study, connectivity refers to how the landscape prevents or facilitates the movement of animals (Taylor et al. 1993). I used indices of connectivity based on graph theory (Cantwell and Forman 1993, Urban and Keitt 2001) to measure the relative connectivity of the anthropogenic sites. The relative connectivity of the natural sites was

not measured because I considered these sites to be completely disconnected (isolated). Graph theory is a branch of mathematics concerned with how networks can be encoded and their properties measured. The term “graph” is not the type that charts data; instead, it is a diagram of the topological patterns and relationships. Graph theory is useful because it can model complexly-connected landscapes as simple arrays of spatial configurations (Cantwell and Forman 1993, Bunn et al. 2000, Urban and Keitt 2001).

I created a graph of the roads at each of my anthropogenic study sites with a set of points (nodes: v) and lines (edges: e). Nodes are placed at every road intersection and terminal point (e.g. a dead end), and edges represent direct connections between nodes (Lowe and Moryadas 1975). In this case, the edges represent the linear anthropogenic habitats. Graph theory provides several indices to quantify the degree of connectivity in a system. I selected two measures that were appropriate to measure the connectivity of my study sites: the gamma and beta indices. These indices were selected because they are the most commonly employed and widely accepted indices of network complexity (Taaffe and Gauthier 1973, Lowe and Moryadas 1975, Cantwell and Forman 1993, Forman 1995). The gamma index measures the percent connectedness and is defined as:

$$\gamma = e/3(v - 2) \quad (1)$$

where e is the number of edges and v is the number of nodes. The gamma index varies from 0 to 1, and can be expressed as a percentage; low values indicate relatively poorer connectivity and large values indicate a relatively higher degree of connectivity (Taaffe and Gauthier 1973, Lowe and Moryadas 1975, Forman and Godron 1986, Rudd et al. 2002). The beta index of connectivity is the average number of edges per node in the network. The beta index is defined as:

$$\beta = e/v \quad (2)$$

where e is the number of edges and v is the number of nodes. Larger beta values indicate higher accessibility and greater complexity (Taaffe and Gauthier 1973, Lowe and Moryadas 1975, Forman and Godron 1986, Cantwell and Forman 1993).

Statistical Analysis

For all analyses in this chapter, I only considered kangaroo rat capture records during the bot fly season (i.e., July 12 to October 13, 2004; see Chapter 2). See Chapter 1 for a detailed description of the study area and kangaroo rat capture methods.

I used Chi-square analysis to assess differences in prevalence among habitat types. Multiple comparisons of prevalence data among the different habitat types were made using the procedure described by Zar (1984: 69-70). Habitat connectivity is a discrete variable on an ordinal scale; therefore, I used a Spearman rank correlation analysis to evaluate the relationships between habitat connectivity and prevalence (and intensity). I used a factorial analysis of variance (ANOVA) to examine the differences in mean intensity among habitat types. When a lack of normality or heteroscedascity was encountered, data were appropriately transformed. I used the capture rate (the number of individuals captured per km surveyed) as a measure of relative kangaroo rat density at each study site. I assessed the relationship between bot fly prevalence and kangaroo rat density with a Spearman rank correlation analysis.

Statistical analyses were performed using SPSS 11.5.1 (SPSS Inc., Chicago, Illinois). Where appropriate, I used a Levene's test to test for homoscedasiticy, one-sample Kolmogorov-Smirnov test with Lilliefors distribution to test for normality of

residuals, and Shapiro-Wilks W test to test for normality. Data are presented as means $\pm$ standard error. I considered alpha levels of 0.05 to be statistically significant.

RESULTS

Measuring Connectivity of Anthropogenic Sites

I measured the relative connectivity for each of the five anthropogenic study sites. There was little variation in the gamma and beta indices; therefore, I divided connectivity into two categories of low and high. The connectivity analysis distinguished three low connectivity road sites from two high connectivity road sites (Table 3.1). Given that the natural sites are relatively discrete, isolated patches of habitat, I considered them to have negligible connectivity compared to the anthropogenic sites. Thus, overall, I had three levels of habitat connectivity: high, low, or none.

Habitat Influences on Bot Fly Parasitism

Table 3.2 presents a summary of the total number of individuals captured, the number parasitized, prevalence, and mean intensity for each study site. Bot fly prevalence was not related to the relative connectivity of habitats (Spearman Rank, $r_s = 0.34$, $n = 10$, $P = 0.34$; Figure 3.1), nor was intensity related to the relative connectivity of habitats ($r_s = 0.20$, $n = 10$, $P = 0.58$).

Prevalence was heterogeneous among the river valley, sand dune, low connectivity road, and high connectivity road habitat types. Mean prevalence at the river valley habitat was only 4.0%, which was significantly lower than sand dunes, low connectivity roads, and high connectivity roads ($\chi^2 = 100.28$, $df = 1$, $P = <0.001$; Figure 3.1). Prevalence was not significantly different among sand dunes, low connectivity

Table 3.1. Results from the connectivity analysis of the anthropogenic study sites. Sites A1, A2, and A5 are less connected than sites A3 and A4. The location of each site is shown in Figure 1.2.

Site name	No. nodes	No. edges	Gamma index	Beta index	Total length (km)	Ranking
A1	2	1	0	0.50	8.9	low
A2	2	1	0	0.50	5.2	low
A5	2	1	0	0.50	5.6	low
A3	8	7	39	0.88	6.2	high
A4	7	6	40	0.86	7.2	high

Table 3.2. Summary of site-specific bot fly parasitism data. Refer to Figure 1.2 for site location. Abbreviations refer to: DUN = sand dune, RV = river valley, and RD = road.

Site name	Habitat type	Connectivity ranking	Total no. individuals	No. parasitized	No. nonparasitized	Prevalence (%)	Mean intensity
N1	DUN	None	12	6	6	50.0	1.7
N2	DUN	None	19	4	15	21.1	1.5
N5	DUN	None	29	20	9	69.0	2.3
N4	RV	None	98	2	96	2.0	1.0
N3	RV	None	101	6	95	5.9	1.0
A1	RD	Low	87	26	61	29.9	1.7
A2	RD	Low	84	36	48	42.9	2.0
A5	RD	Low	69	38	31	55.1	1.8
A3	RD	High	35	18	17	51.4	1.6
A4	RD	High	36	16	20	44.4	1.6

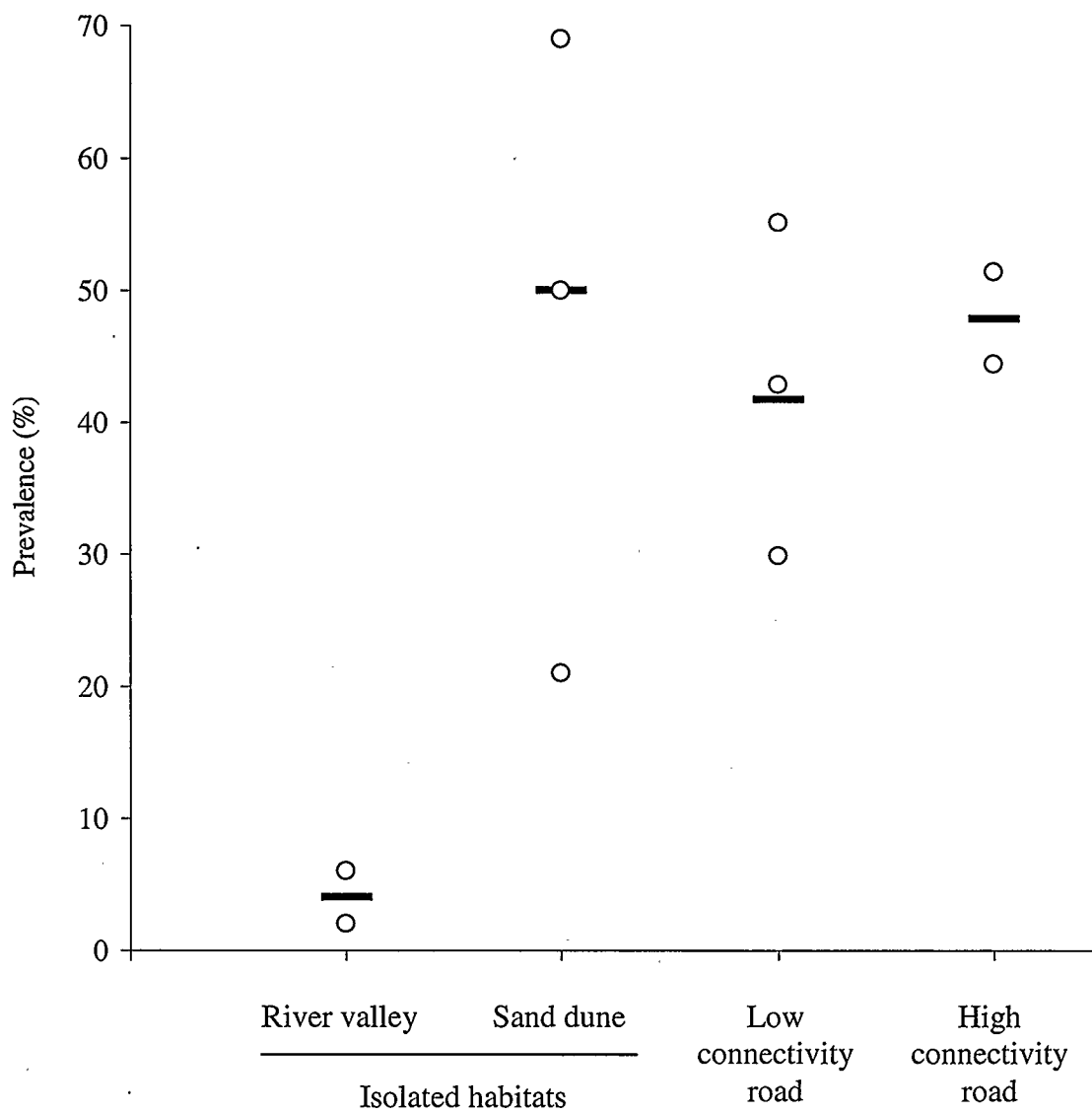


Figure 3.1. Bot fly prevalence for the different habitat types. The points (○) indicate the actual prevalence values from each site and the bars (—) indicate the mean values of sites at each habitat type.

roads, and high connectivity roads ($\chi^2 = 1.63$, $df = 2$, $P = 0.44$; Figure 3.1). The sand dune habitat type had the most variable parasitism rates among sites: prevalence was 21.1%, 50.0%, and 69.0% at each of the three sand dune sites (Table 3.2 and Figure 3.1).

Whereas, at the other habitat types prevalence among sites was more homogeneous.

In my analysis of intensity and habitat type, it was necessary to remove the river valley habitat type because of small, within-group sample size and lack of variance (i.e., each parasitized individual had an intensity = 1). Additionally, the intensity data did not meet the assumption of normality, even with transformation. However, an ANOVA was still used because it is robust to lack of normality (Zar 1984: 170) and the data satisfied the assumption of homogeneity of variances. Using untransformed data, the intensity of parasites was not significantly different among sand dunes, low connectivity roads, or high connectivity roads (ANOVA; $F = 1.28$, $df = 2$, 161, $P = 0.28$; Figure 3.2).

The density of kangaroo rats at each study site was not correlated with either prevalence or intensity (Spearman rank correlation, $r_s = -0.382$, $n = 10$, $P = 0.276$ and $r_s = -0.395$, $n = 10$, $P = 0.258$ for prevalence and intensity, respectively; Figure 3.3).

DISCUSSION

This is the first study to document the spatial pattern of *C. polita* infection in Ord's kangaroo rat. I have shown that in the SNWA, bot fly prevalence in kangaroo rats differs significantly among habitat types. However, my predictions were not supported. Bot fly prevalence and intensity were not significantly associated with habitat connectivity. As well, prevalence and intensity were not significantly higher at anthropogenic habitat. The results showed that kangaroo rats occupying roads and sand

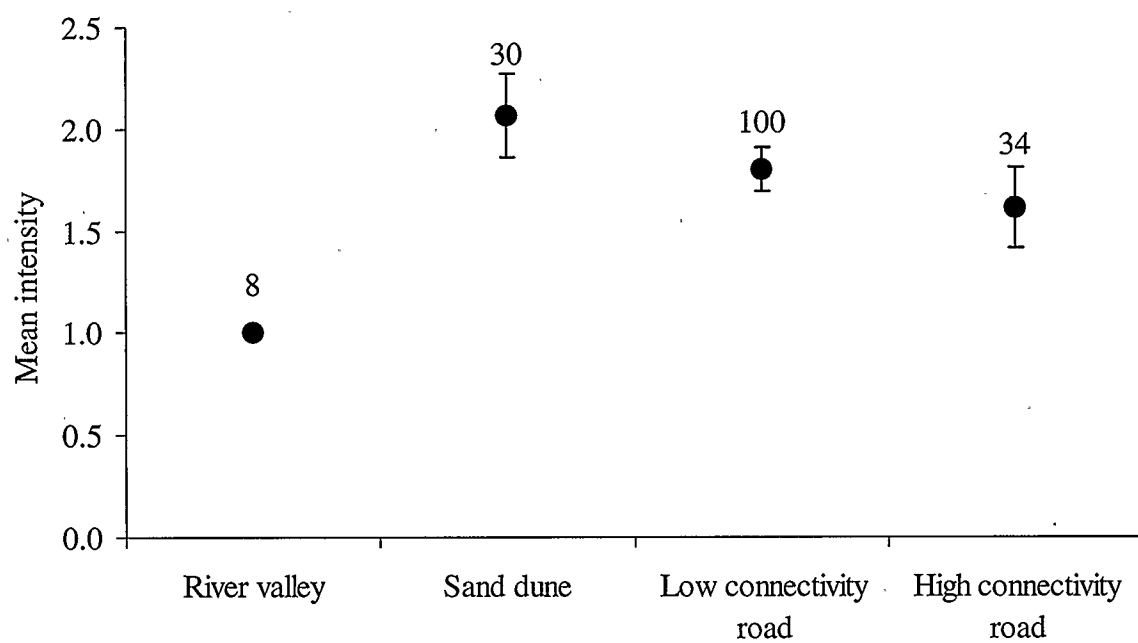


Figure 3.2. The mean number of parasites per Ord's kangaroo rat (intensity) at the different habitat types. The sample size is shown above and error bars indicate $\pm$ standard error. Intensity at the river valley habitat type was not included in the analysis but is shown here for comparison.

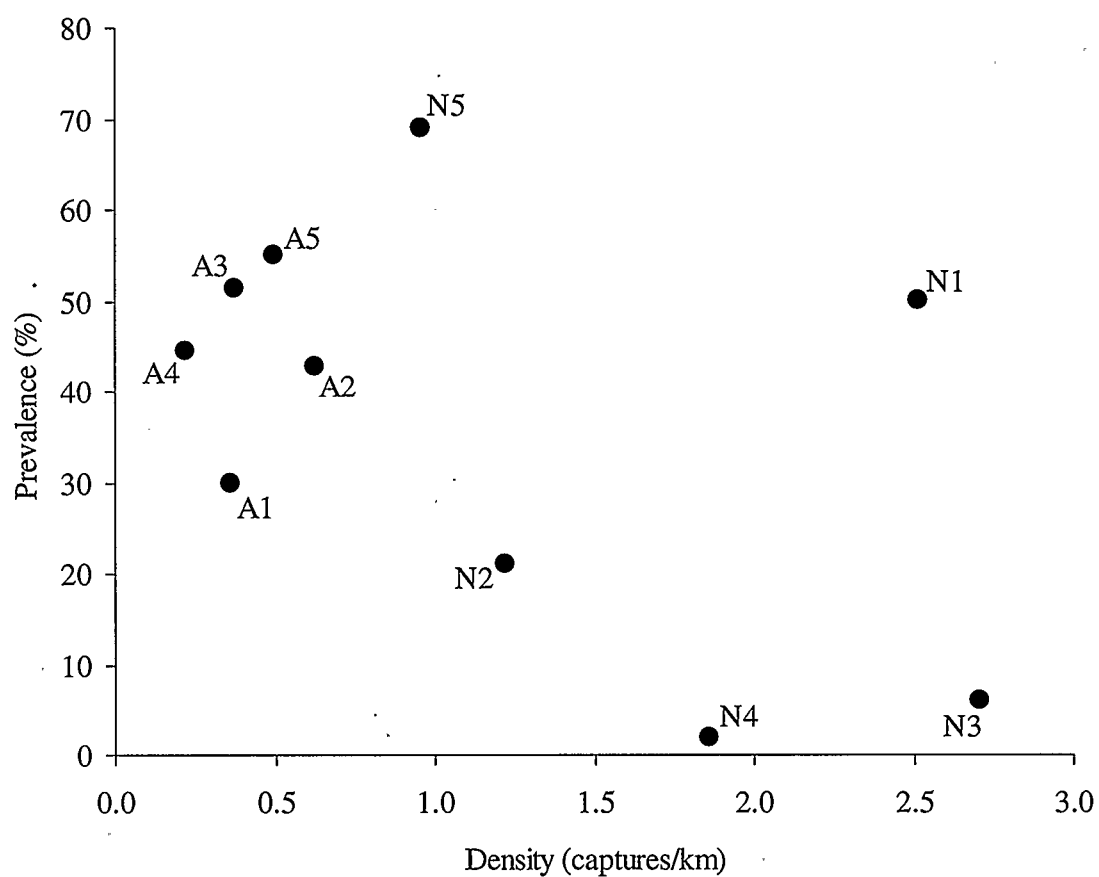


Figure 3.3. Prevalence of bot fly parasitism at each study site as a function of the relative density (number of kangaroo rats captured per km surveyed) of Ord's kangaroo rats.

dunes experienced significantly greater bot fly prevalence than kangaroo rats at the river valley habitat. Prevalence was variable among the three sand dune sites, varying from 21% to 69%, whereas prevalence was more consistent within each of the other habitat types. In part, the variability of prevalence at dune sites is due to low numbers of kangaroo rats living at these locations, thus some uncertainty exists for dunes. It should also be noted that low prevalence was observed at sand dunes between 1999 and 2002 during previous studies of kangaroo rats in Alberta (Figure 1.1), apparently contradicting my findings. However, natural sites were under-represented in these years (D. Gummer, personal comm.) which may partially explain the discrepancy. Alternatively, parasitism rates at dunes in 2004 may have been uncharacteristically high.

Kangaroo rats were parasitized in all habitat types, although prevalence at the river valley habitat was significantly lower. Possible factors that may have influenced prevalence include host density (Brigada et al. 1992, Wilson et al. 1997), transient movement of individuals (Miller and Getz 1969), microclimate and habitat availability (Getz 1970, Wolf and Batzli 2001), and burrow visibility (Capelle 1970, Graham and Capelle 1970).

Parasite prevalence is typically related to host population density (Jones 1967). For example, bot fly prevalence was found to be positively correlated with the density of the shrubland mouse (*Akodon molinae*; Brigada et al. 1992). However, in this study bot fly prevalence was not associated with kangaroo rat density, supporting the findings of previous research by Miller and Getz (1969), Bennett (1972), Hensley (1976), Boggs et al. (1991), and Wilson et al. (1997). Interestingly, three of the four highest density sites had the lowest prevalence.

A very small number of kangaroo rats were parasitized at the river valley sites. Is it possible that these were transient individuals that were emigrating from areas with high bot fly prevalence? This does not seem likely based on capture records of the parasitized individuals at the river valley sites. These parasitized individuals were recently emerged juveniles or had multiple captures in the same location, suggesting that they were residents. For this reason, I am confident that the low prevalence observed at the river valley sites is characteristic of this type of habitat rather than from the absence of adult bot flies or immigration of parasitized individuals.

Microclimatic conditions or availability of suitable habitat for *C. polita* probably does not elucidate why prevalence was significantly lower at the river valley sites. Bot fly eggs are resistant to environmental factors (Catts 1967, Bennett 1972), and hence, there is no obvious reason that eggs laid inside kangaroo rat burrows at the river valley habitat would not have survived. Furthermore, differences in microclimate characteristics did not appear to influence the presence of bot flies in previous studies. For instance, Getz (1970) found no difference in soil moisture and temperature, light penetration, surface temperature, and relative and absolute humidity between two habitats with different bot fly prevalence. The presence of adult *Cuterebra* appears to be more related to the presence of adequate aggregation sites, i.e. areas where adult bot flies congregate for mating opportunities (Hensley 1976, Boggs et al. 1991). The known aggregation site of *C. polita* is reported to be stepped slopes (Catts 1982), which, interestingly, is the type of habitat along the river valley that had the lowest level of parasitism.

A possible, albeit speculative reason for significantly lower prevalence at the river valley habitat was that adult female *C. polita* may have been unable to locate the burrows

of kangaroo rats. Despite the fact that the river valley sites had very high concentrations of kangaroo rats, they were also more densely vegetated than other sites. The river valley sites appeared to have more vegetation cover around the burrows, and thus kangaroo rat burrows were noticeably less visible (at least to humans), whereas at sand dunes and along roadways burrows appeared very conspicuous. Whether the difference in burrow visibility is relevant to bot fly parasitism rates in kangaroo rats needs to be tested and future studies will be required to understand why the natural habitat sites experienced such unexpectedly different degrees of parasitism.

The differences in bot fly prevalence among road, sand dune, and river valley habitat raises the question of whether bot fly parasitism affects the life history traits of kangaroo rats. In the next chapter, I examine the potential impact of bot fly parasitism on kangaroo rat body condition, reproduction, and survival. As well, I examine if there is an interaction effect between bot fly parasitism and habitat type on body condition, reproduction, and survival.

CHAPTER 4

EFFECTS OF BOT FLY PARASITISM ON BODY CONDITION, REPRODUCTION, AND SURVIVAL OF THE ORD'S KANGAROO RAT

INTRODUCTION

Studies of bot fly (*Cuterebra* spp.) parasitism in natural hosts, such as the white-footed mouse (*P. leucopus*) and deer mouse (*P. maniculatus*), tend to show that infection has a modest effect on the fitness of its host (Hunter and Webster 1974, Smith 1978, Timm and Cook 1979, Timm and Lee 1981, Munger and Karasov 1991, 1994, Burns et al. 2005, Jaffe et al. 2005). The relationship may not be as benign, however, for atypical hosts, resulting in detrimental effects on host body mass, reproduction, and survival (Catts 1965, Jacobson et al. 1978, Catts 1982).

Effects on Body Condition

Bot fly larvae consume the host's living tissue and exudate (Payne and Cosgrove 1966, Catts 1982, Colwell et al. 2006). During the relatively short infection period, the larvae must increase its body mass 100 000-fold prior to leaving the host (Catts 1982). As a result, parasitized animals may have to decrease their growth or fat storage to compensate for the energetic costs of the parasite (Munger and Karasov 1994).

In most cases, bot fly parasitism does not cause significant weight loss in natural hosts, but in atypical hosts, weight loss can be substantial (Catts 1982). In a parasite-host specificity study, Catts (1965) observed: 1) significant weight loss in atypical hosts (laboratory mice, *Mus musculus* and hamsters, *Cricetus auratus*); 2) gradual, but not significant, weight loss in one natural host (deer mice) and; 3) no weight loss in a second

natural host (dusky-footed wood rat, *Neotoma fuscipes*) even when supporting heavy parasite loads.

Effects on Reproduction

The energetic costs and physical hindrance of bot fly parasitism may affect the reproductive potential of the host through temporary sterility, physical and behavioural changes, and mechanical hindrance to copulation (Hensley 1976, Smith 1977b).

Additionally, parasitized females may not become pregnant and those that do may be forced to absorb embryos or they may not be able to successfully wean their young (Sillman 1955, Sealander 1961, Smith 1977b, Timm and Cook 1979).

The effect of bot fly parasitism on reproduction of atypical hosts has not been investigated, and the results from studies of natural hosts are contradictory in the literature. For example, one study reported that bot fly parasitism drastically reduced the rate of lactating and pregnant adult female voles (Iverson and Turner 1968, Boonstra et al. 1980), whereas another study reported that almost half of the parasitized female voles were pregnant (Getz 1970). Contradictory results also exist in studies of the white-footed mouse. For instance, Hensley (1976) reports that significantly fewer parasitized females were reproductively active compared to nonparasitized females, while Munger and Karasov (1991) and Burns et al. (2005) did not find a reduction in reproductive activity of parasitized female mice. However, Burns et al. (2005) examined the number of litters and litter size of white-footed mice, and found that parasitized females produced fewer litters and offspring than nonparasitized females, even though parasitized females displayed external signs of breeding. For this reason, Burns et al. (2005) suggest that external signs of reproductive condition may not be a good indicator of reproductive success.

Reproductive activity of parasitized males is reported to be affected because bot fly larvae are often located in the inguinal (groin) region of the host. Larvae positioned in the inguinal region can cause the testes to be displaced and, in some cases, apparent castration has been reported (Dalmat 1943, Wecker 1962, Dunaway et al. 1967, Hensley 1976). Timm and Lee (1982) investigated the notion of host castration by bot flies, and they concluded that testicular descent can be inhibited, but host castration does not occur. Conversely, Munger and Karasov (1991) did not observe a difference in reproductive activity between parasitized and nonparasitized males.

Effects on Survival

Survival of animals parasitized by bot fly larvae may be reduced directly or indirectly. Direct mortality may occur during migration of first instar larvae or when mature larvae vacate the host (Smith 1977a, Catts 1982). Indirect mortality may occur through reduced mobility, which may increase predation risk and inhibit the collection of adequate over-winter food stores (Smith 1978b).

Direct mortality

Bot fly larvae instinctually follow a migration route through the body of their natural host (Gingrich 1981). In atypical hosts, severe internal damage can result from aberrant movement by first instar larvae, which can kill the host (Catts 1982). In laboratory studies, mortalities of animals shortly after exposure to first instar larvae were suspected to have occurred from aberrant movement of the larva (Catts 1965, Baird 1971).

High rates of mortality were also observed during laboratory studies due to severe tissue damage at the warble pore after the mature larvae vacated the host (Smith 1977a,

Baird 1979). Smith (1977a) observed that in atypical hosts, direct mortality following larval exit was high, ranging from 62.5% to 95.5%, although the rate of mortality in the natural host was not reported. Mortality during larval exit has also been observed in a limited number of cases in natural hosts (Dalmat 1943, Bennett 1973).

High rates of mortality in atypical hosts have also been reported during host specificity laboratory studies where the actual cause of death was unknown. Gingrich and Barrett (1976) reported 'excessive' mortality in gerbils (*Gerbillus gerbillus*) and laboratory mice infected with *C. fontinella* (i.e., the natural parasite of white-footed mice). In another study, the mortality rate of atypical hosts infected with *C. tenebrosa* was 7% in laboratory mice, 20% in laboratory rats (*Rattus norvegicus*), and 50% in dusky-footed woodrats, while mortality in the natural host, bushy-tailed woodrats (*N. cinerea*), was only 4% (Baird 1979).

Indirect mortality

Bot fly larvae are relatively large parasites that are located under the skin of their host, as a result they could interfere with the host's mobility (Scott and Snead 1942, Sealander 1961, Dunaway et al. 1967) and therefore indirectly impact the host's survival. Reduced mobility could affect the host in two ways: First, reduced mobility could inhibit the host's ability to escape predators (Wecker 1962, Dunaway et al. 1967, Smith 1978ab, Steen et al. 2002). For example, deer mice carrying two or more bot fly larvae were unable to escape predators (Smith 1978b). Second, reduced mobility could hinder the host's ability to collect and store an adequate over-winter food cache, thereby leading to over-winter starvation.

Application to an Atypical Host

The kangaroo rat is considered an atypical bot fly host for two reasons: First, the bot fly and the kangaroo rat have extensive range overlap in North America (Figure 4.1), and despite broad ranging and extensive studies, the Canadian kangaroo rat population is the only one reported to be parasitized by bot flies (Gummer et al. 1997). Second, bot fly parasitism has not previously been documented in the genus *Dipodomys*.

As an atypical host, kangaroo rats parasitized by bot fly larvae may experience significant weight loss. This is an important consideration for the northern kangaroo rat population because any potential loss of body mass as a result of parasitism could lead to reduced fat stores necessary for over-winter survival (Gummer 1997a, Gummer et al. 1997).

In Alberta, adult kangaroo rats begin to reproduce in the early spring, and typically continue to do so throughout the summer, and juveniles may reproduce in their first summer (Gummer 1997a). According to Gummer (1997a), the Canadian kangaroo rat population invests significant resources toward reproduction because of low survival. However, the energetic costs and physical hindrance of bot fly parasitism may impact the reproduction of kangaroo rats. Specifically, the energetic costs of parasitism may induce kangaroo rats into a non-reproductive state and juvenile kangaroo rats may need to delay sexual maturity. As well, the physical hindrance of parasitism may impact the reproductive success of kangaroo rats. Bot fly parasitism may coincide with the breeding season of the kangaroo rat, and a negative influence of bot fly parasitism on reproduction could drastically impact the population dynamics through a reduction in offspring.

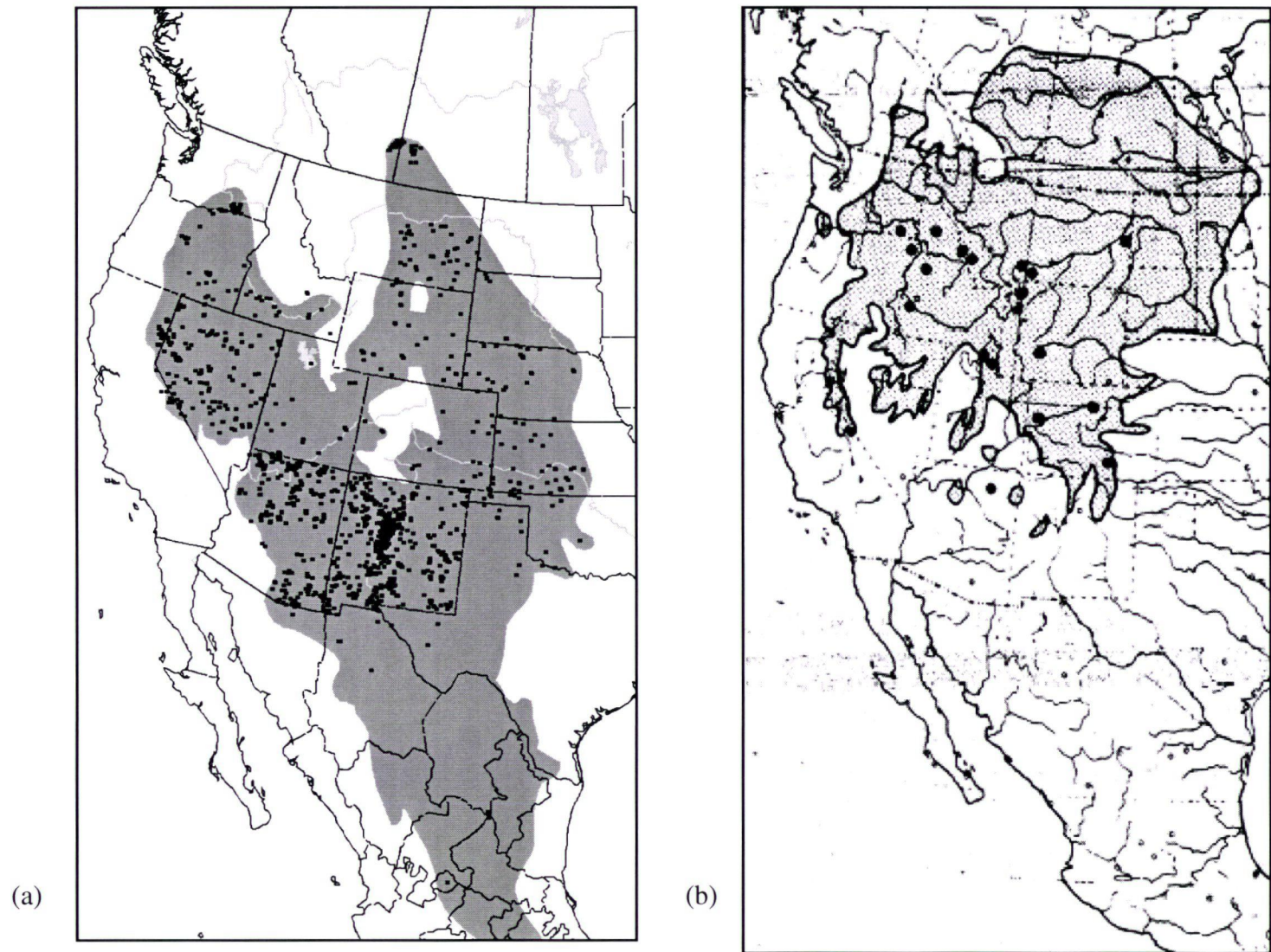


Figure 4.1. Range of the Ord's kangaroo rat (*Dipodomys ordii*) (a; modified from Hall 1981) and *Cuterebra polita* (b; from Sabrosky 1986: 132).

Kangaroo rats have a variety of predators, such as the coyote (*Canis latrans*), red fox (*Vulpes vulpes*), long-tailed weasel (*Mustela frenata*), badger (*Taxidea taxus*), prairie rattlesnake (*Crotalus viridis viridis*), short-eared owl (*Asio flammeus*), and great horned owl (*Bubo virginianus*). One technique that kangaroo rats use to evade predators is to jump around erratically in an unpredictable zig-zag pattern when pursued (Bartholomew and Caswell 1951). Kangaroo rats carrying one or more bots may experience reduced mobility and be unable to escape predators as efficiently as nonparasitized animals.

Kangaroo rats are granivorous and are not active above ground during the winter. Instead, they rely on underground food stores (Gummer 1997a). In order for kangaroo rats to survive the winter, they must cache sufficient amounts food to meet their energy requirements (Gummer 1997a). If parasitized kangaroo rats experience reduced mobility, they may not be able to gather enough food for over-winter storage, and are therefore more prone to starvation.

Research Objectives

The objective of this study was to determine the effects of bot fly parasitism on the body condition, reproduction, and survival of kangaroo rats. I predicted that bot fly parasitism will adversely affect the body condition, reproduction, and survival of kangaroo rats as a result of the atypical host-parasite relationship.

METHODS

To analyse the effects of parasitism on body condition and reproduction, I used kangaroo rat capture records during the bot fly season only (i.e., July 12 to October 13, 2004; see Chapter 2). For the survival analysis, I used mark-recapture data collected

during July 12 – October 21, 2004, and April 28 – August 1, 2005. For a review of the study area and kangaroo rat capture methods, see Chapter 1.

I used an analysis of covariance (ANCOVA) to analyse the effect of parasitism on body condition, chi-square, and logistic regression to analyse the effect of parasitism on reproduction, and logistic regression and Cormack-Jolly-Seber models to analyse the effect of parasitism on survival. The parasitism status of an individual was parasitized or nonparasitized. The intensity of parasites was the maximum number of larvae, empty warble pores, and scars an individual had at one time. I analysed the possible effects of parasitism status and intensity on body condition, reproduction, and survival separately.

Habitat type was included as a predictor variable in each analysis because of potential differences in habitat quality. I considered the roads to be poorer quality habitat than natural areas (i.e., sand dunes and river valley areas) because of higher predation risk and lower food quality. Predators such as coyotes and owls can be abundant along roads (Simberloff and Cox 1987, Forman 1995, Zimmerman et al. 1996). Additionally, food quality was presumably poorer because of the presence of exotic plant species along roads in the study area (Adams et al. 1997). Therefore, the potential harmful effects of parasitism may be exacerbated for kangaroo rats living along roads.

I pooled the low and high connectivity roads because prevalence and intensity did not differ between them (see Chapter 3). Consequently, I compared three different habitat types: river valley, sand dune, and road (unless stated otherwise). Sex was included as a predictor variable in the analysis of body condition because kangaroo rats are sexually dimorphic (Best 1993, Gummer 1997a). As well, I wanted to test for differential survival between the sexes, so sex was included as a predictor variable in the survival analysis.

Body condition may contribute to variation in reproductive status and survival, thus it was included in these analyses as well. The specific method used for each analysis is described in detail below.

Effects on Body Condition

I computed a body mass index (BMI) to assess if bot fly parasites affect the fitness of kangaroo rats. The BMI determines the mass after correcting for structural body size, thereby providing an indicator of relative body condition (Schulte-Hostedde et al. 2005). A common method used to derive a BMI is to regress body mass against some linear measure of body size and using the residuals from the regression (Krebs and Singleton 1993, Jakob et al. 1996, Schulte-Hostedde et al. 2005). A positive residual indicates better-than-average condition, and a negative residual indicates a poorer-than-average condition (Jakob et al. 1996, Schulte-Hostedde et al. 2001, 2005).

Ordinary least squares (OLS) regression is commonly used to derive body condition indices. However, the use of OLS regression has recently been debated and evaluated. Green (2001) suggested the use of reduced major axis (RMA) regression and major axis (MA) regression instead of OLS regression because of the violation of key assumptions. Specifically, OLS regression assumes that the independent variable is independent of the dependent variable and there is no error in the independent variable, and RMA and MA regressions assume that error occurs in both the independent and dependent variables (Sokal and Rohlf 1995). Schulte-Hostedde et al. (2005) evaluated these methods and found that OLS regression is a better method than RMA and MA regressions for small mammals because OLS regression predicted body composition better, also it was a better predictor of body mass (Schulte-Hostedde et al. 2005).

In this study, the tail length of kangaroo rats was used as a measure of body size because it is easy to measure in the field and tightly correlated with overall skeletal length (Teucher in prep.). Body mass and tail length were transformed using natural logarithms and the relationship between the transformed variables was described using OLS regression analysis (Schulte-Hostedde et al. 2005). I used the coefficients from the regression analysis to calculate a predicted body mass for each individual, and then I calculated BMI as the observed body mass minus the predicted body mass. I calculated BMI separately for adults and juveniles due to different growth rates.

I compared BMI between parasitized and nonparasitized individuals with an ANCOVA; the date on which mass was recorded was the covariate. In the intensity analysis, intensity was used as a covariate. To make the groups more homogeneous, I excluded kangaroo rats at the river valley habitat type because of small, within group sample sizes (< 5 parasitized individuals). Therefore, the habitat type variable consists of two different habitat types: sand dunes and roads. I excluded pregnant females from the analysis. Adults and juveniles were analysed separately.

Effects on Reproduction

Individual-level analysis

I examined potential effects of bot fly parasitism on reproduction by examining the proportion of parasitized and nonparasitized kangaroo rats observed to be reproductively active. In this analysis, females that were estrous, pregnant, or lactating were considered reproductively active and all others were considered not active. I considered males with descended testes to be reproductively active and all others not active. Nonparasitized individuals had to be observed reproductively active at least once

during the bot fly season to be considered active. I used the reproductive condition during the parasitism event for parasitized individuals. Therefore, captures prior to the parasitism event were disregarded. An individual was counted only once, and those with an unknown reproductive condition were removed.

I examined the relationship between bot fly parasitism and reproductive status (active or not active) using chi-square analysis and logistic regression. In the logistic regression analysis, reproductive status was coded as 1 (reproductively active) and 0 (not reproductively active). I also included one categorical variable (habitat type) and two continuous variables (BMI and date the reproductive condition was observed) in the model. As well, I added the interaction between these variables and parasitism status/intensity. Model selection using an information theoretic approach, such as Akaike's information criterion (AIC), is not appropriate when modeling a mix of categorical and continuous predictor variables in a logistic regression model (Quinn and Keough 2002). Therefore, I used an alternative method for model selection, the forward stepwise procedure, which allowed me to use both categorical and continuous predictor variables in my logistic regression. I used a forward stepwise procedure with the log-likelihood ratio and the criteria $\alpha = 0.05$ to enter and $\alpha = 0.10$ to remove. I tested the suitability of the logistic regression model using a Hosmer and Lemeshow test for goodness-of-fit, where $P > 0.05$ indicates that the model prediction does not significantly differ from the observed data (Quinn and Keough 2002). I tested males and females separately.

Population-level analysis

I examined the potential effects of bot fly prevalence on juvenile recruitment. I estimated juvenile recruitment because I could not measure reproductive success directly. I defined juvenile recruitment as the ratio of juveniles to adult females observed to have shown evidence of breeding (i.e., pregnant, lactating, or post-lactating; Krebs 1966, Sullivan et al. 2005). The majority of adult females in my study displayed breeding evidence. Incidentally, the ratio of juvenile to adult female density has been used to examine reproductive success (Van Horne et al. 1997). In my study it was important to consider only juveniles whose mothers may or may not have been affected by bot fly parasitism. I selected juveniles based on a model that predicted their date of birth (see Gummer 1997); juveniles estimated to be born prior to or during the bot fly season were considered recruits. I am assuming that the number of juveniles captured reflects the number of juveniles that were actually recruited, yet the likelihood that all juveniles were captured may be low. However, I do not expect the capture success to be different between juvenile recruits from parasitized or nonparasitized mothers. I used a Spearman rank correlation analysis to evaluate the relationship between juvenile recruitment and bot fly prevalence at each study site. I excluded two sites (N1 and A5) from this analysis because survey effort began too late in the breeding season to adequately determine the ratio of juveniles to adult females.

Effects on Survival

I compared survival between parasitized and nonparasitized kangaroo rats captured in the bot fly season to the following year using logistic regression (individual-level analysis) and mark-recapture methods (population-level analysis). I assumed that

capture success was equal for parasitized and nonparasitized kangaroo rats, and that individuals not recaptured had died (Waser and Jones 1991). Perhaps this latter assumption underestimates survival, but adult kangaroo rats exhibit high site fidelity and rarely move long distances from the point of first capture (Eisenberg 1963, Garrison and Best 1990, Jones 1993, Gummer 1997a).

Individual-level analysis

I measured survival at two levels: overall survival and over-winter survival. Overall survival was the proportion of individuals captured during the bot fly season in 2004 that were recaptured in the spring/summer 2005. Over-winter survival was the proportion of individuals captured in September and October 2004 that were recaptured in spring/summer 2005. I coded survival as 1 or 0 (recaptured in 2005 or not recaptured in 2005, respectively).

Overall survival analysis

The model included sex, habitat type, and BMI, as well as the interaction of these variables with parasitism status (and intensity). I used a forward stepwise procedure with the log-likelihood ratio and the criteria $\alpha = 0.05$ to enter and $\alpha = 0.10$ to remove. I tested adults and juveniles separately. Kangaroo rats at site A5 were removed from the survival analysis due to unanticipated circumstances at this site only; cattle were released in this area in the fall of 2004. I felt it was necessary to remove this site because I cannot be sure that the cattle did not affect kangaroo rat survival. Cattle tend to congregate along roads and may trample kangaroo rats in their burrows.

Over-winter survival analysis

I considered only the individuals that were known to be alive in the fall to better assess the potential effects of bot fly parasitism on over-winter survival of kangaroo rats. This greatly reduced the sample size, so habitat type had to be removed as a predictor variable. I also excluded the individuals at the river valley habitat (sites N3 and N4) since no parasitized individuals were captured during the fall. Therefore, only sex and BMI, along with parasitism status (and intensity), were included in the logistic regression model. A Fisher's Exact test was used to examine survival between parasitized and nonparasitized juveniles because of small sample size.

Population-level analysis

I further examined survivorship of kangaroo rats with Cormack-Jolly-Seber (CJS; Cormack 1964, Jolly 1965, Seber 1965) models in Program MARK (White and Burnham 1999). In Program MARK, CJS models estimate apparent survival (Φ) and recapture probabilities (p) separately with maximum likelihood techniques (White and Burnham 1999, White et al. 2001). Apparent survival is the probability that an animal survives from one capture occasion to the next and does not emigrate from the study area; recapture probability is the probability that a live animal in the study area during the survey time is caught during that survey (Cooch and White 2005). MARK does not differentiate between permanent emigration and death, thus animals that emigrate are assumed to have died.

I categorized the data into eight groups based on parasitism status, sex, and habitat type. The river valley habitat was removed due to a small, within group sample size. I modeled adults and juveniles separately. Data from each lunar period (centered on

the new moon) during the bot fly season was pooled into one capture occasion. Therefore, capture histories were made up of six intervals. I examined combinations of parasitism status, habitat type, sex, and time as sources of variation in survival and recapture rates. The global model (a model that includes all the parameters considered to be important) and a range of alternative models were run using the logit link function in MARK (Table 4.1; Cooch and White 2005). I did not test all possible combinations of predictor variables because it is ideal to keep the number of candidate models to a minimum, modeling only biologically meaningful models and models of interest (Burnham and Anderson 1998). Therefore, I used the approach described in Lebreton et al. (1992), modeling recapture first to determine the best model for recapture rates, and then modeling survival rates using the best parameterization of recapture rates.

It is an important first step to ensure that the global model adequately fits the data. MARK offers various methods to evaluate the fit of the global model. I used the median $\hat{c}$ method described in Cooch and White (2005), where $\hat{c}$ is a measure of overdispersion in the data. Overdispersion occurs when the assumptions underlying the model have not been met, such as heterogeneity in survival or recapture rates among individuals. When $\hat{c}$ is equal to 1, the model fits the data. If $\hat{c}$ is greater than 1, overdispersion exists.

I selected models on the basis of AIC selection. AIC is an information theoretic approach that ranks models in a candidate set based on model fit (deviance) and parsimony (measured by the number of parameters; Burnham and Anderson 1998, Cooch and White 2005). The goal is to identify a biologically significant model that adequately

Table 4.1. Models used to describe survival and recapture rates. Abbreviations refer to: h = habitat, i = parasitism status, s = sex, and t = time period (sampling period, centered around the new moon). Models denoted as h*t include the two main effects and the interaction term. Models denoted as h+t are additive models and do not include an interaction term.

Model Notation	Biological significance
(h*i*s*t)	Parasitized and nonparasitized females and males at different habitats have different survival (or recapture) rates that are time dependent.
(h*i*t)	Parasitized and nonparasitized individuals at different habitats have different survival (or recapture) rates that are time dependent.
(h*s*t)	Females and males at different habitats have different survival (or recapture) rates that are time dependent.
(h*t)	Individuals at different habitats have different survival (or recapture) rates that are time dependent.
(h+i+s+t)	Survival (or recapture) rates depend on habitat, parasitism status, sex, and time.
(h+i+t)	Survival (or recapture) rates depend on habitat, parasitism status, and time.
(h+s+t)	Survival (or recapture) rates depend on habitat, sex, and time.
(h+t)	Survival (or recapture) rates are habitat and time dependent.
(h)	Survival (or recapture) rates depend on habitat only.
(i*s*t)	Parasitized and nonparasitized females and males have different survival (or recapture) rates that are time dependent.
(i*t)	Parasitized and nonparasitized individuals have different survival (or recapture) rates that are time dependent.
(i+s+t)	Survival (or recapture) rates depend on parasitism status, sex, and time.
(i+t)	Survival (or recapture) rates depend on parasitism status and time.
(i)	Survival (or recapture) rates depend on parasitism status only.
(s*t)	Females and males have different survival (or recapture) rates that are time dependent.
(s+t)	Survival (or recapture) rates depend on sex and time.
(s)	Survival (or recapture) rates depend on sex only.
(t)	Survival (or recapture) rates depend on time only.
(.)	Survival (or recapture) rates are constant over time.

explains the variation in the data while minimizing the number of parameters. I used AIC corrected for overdispersion and small sample size, referred to as the quasi Akaike's information criterion (QAIC; Burnham and Anderson 1998, White et al. 2001, Cooch and White 2005). QAIC is calculated as: $QAIC = -2\ln L/\hat{c} + 2K$, where $\ln L$ is the log-likelihood, $\hat{c}$ is the variation inflation factor estimating the overdispersion of the data, and K is the number of parameters. The model with the lowest QAIC is considered the 'best' model in the set. Program MARK provides QAIC, differences in QAIC ($\Delta QAIC$) among the top and alternative models, Akaike's weight, number of parameters, and deviance for each model. Models $\leq 2 \Delta QAIC$ are considered to have substantial support and should also be used for making inferences (Burnham and Anderson 1998). Models with a $\Delta QAIC$ of 4–7 have considerably less support and models with $\Delta QAIC > 7$ have essentially no support (Burnham and Anderson 1998). Akaike weights can also be used to select the 'best' model in the set. The Akaike weight is the probability of being the actual best model in the set, the larger the $\Delta QAIC$, the smaller the weight and the less likely is the alternative model (Buckland et al. 1997, Burnham and Anderson 1998).

Effects on movement

Other researchers have speculated that bot fly parasitism does not have a negative impact on the survival of the host because parasitized animals move less than nonparasitized animals, thus emigrating less often and decreasing predation risk (Wecker 1962, Burns et al. 2005). I examined the maximum recapture distance (MRD: the distance between the furthest capture locations) for individuals with two or more capture locations. I compared the maximum recapture distance between a comparable group of parasitized and nonparasitized kangaroo rats with a t test. Additionally, I compared the

distribution of the maximum recapture distance between parasitized and nonparasitized kangaroo rats with a Kolmogorov-Smirnov test (Burns et al. 2005).

I performed statistical analyses with SPSS 11.5.1 (SPSS Inc., Chicago, Illinois) and Program MARK (White and Burnham 1999). Where appropriate, I used a Levene's test for homoscedasticity and a one-sample Kolmogorov-Smirnov test with Lilliefors distribution to test for normality of residuals. All tests were 2-tailed with a significance level of $P = 0.05$. All means are expressed $\pm$ standard error.

RESULTS

Effects on Body Condition

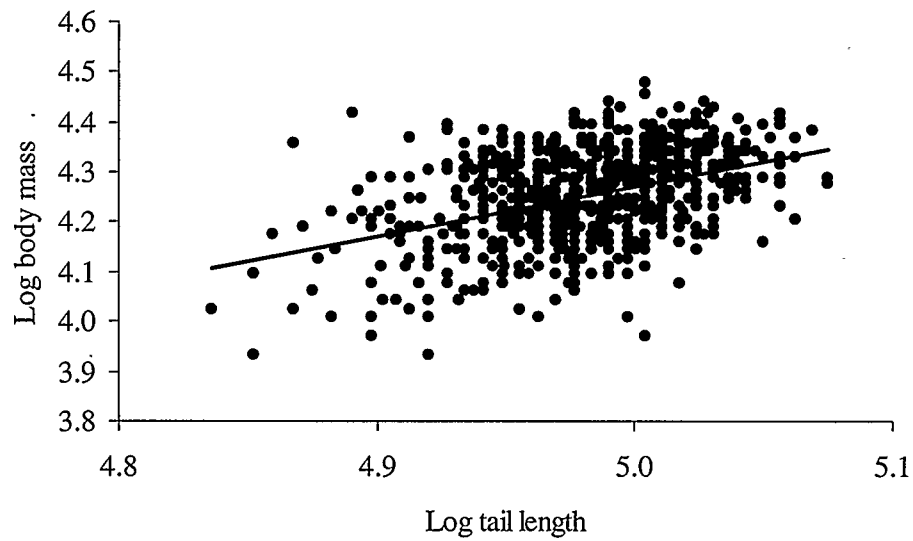
The relationship between body mass (BM) and tail length (TL) was significant ($P < 0.001$) for adults ($n = 754$) and juveniles ($n = 386$). Linear regression models for adult and juvenile kangaroo rats are as follows:

Adult: $\ln \text{BM} = -0.787 + 1.012 \ln \text{TL}$, $R^2 = 0.174$ (Figure 4.2a)

Juvenile: $\ln \text{BM} = -4.145 + 1.650 \ln \text{TL}$, $R^2 = 0.793$ (Figure 4.2b)

The BMI of adult kangaroo rats was not associated with bot fly parasitism or interactions between parasitism status and sex or parasitism status and habitat type (Table 4.2 and 4.3). The BMI was significantly different between adult males and females (Table 4.2; Figure 4.3). There was marginal significance of BMI between the two habitat types; the mean BMI was 0.037 ± 0.014 and 0.009 ± 0.006 for sand dunes and roads, respectively. Similarly for juveniles, bot fly parasitism did not have a significant effect on the BMI and there was no significant interaction between parasitism and habitat type

a)



b)

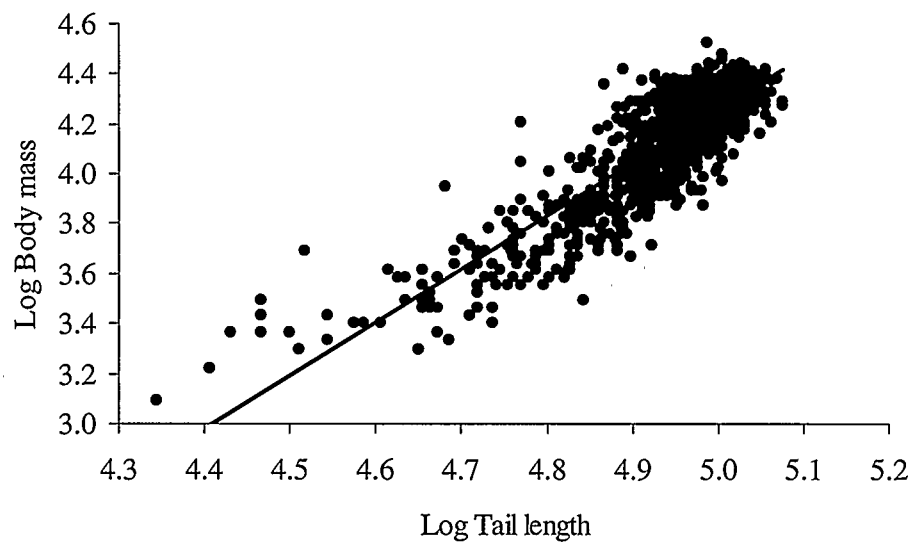


Figure 4.2. Relationship between ln-transformed body mass (BM) and ln-transformed tail length (TL) for adult (a) and juvenile (b) Ord's kangaroo rat. The line indicates the best fitting line determined by ordinary least squares regression analysis and is described as: $\ln \text{ BM} = -0.787 + 1.012 \ln \text{ TL}$, $R^2 = 0.174$ for adults and $\ln \text{ BM} = -4.145 + 1.650 \ln \text{ TL}$, $R^2 = 0.793$ for juveniles.

Table 4.2. ANCOVA for the effects of parasitism status (parasitized or nonparasitized), sex, and habitat type (sand dune and road) on the body mass index (BMI) of adult and juvenile Ord's kangaroo rats. The date mass was recorded was used as a covariate.

Source of variation	Sum of squares	Df	Mean square	F-ratio	P
Adult					
Date	0.002	1	0.002	0.285	0.594
Parasitism status	0.001	1	0.001	0.189	0.664
Sex	0.068	1	0.068	9.885	0.002
Habitat type	0.019	1	0.019	2.781	0.097
Parasitism status*Sex	0.000	1	<0.001	0.071	0.790
Parasitism status*Habitat type	<0.001	1	<0.001	0.006	0.938
Sex*Habitat type	0.015	1	0.015	2.157	0.143
Parasitism status*Habitat type*Sex	0.002	1	0.002	0.236	0.628
Error	1.405	203	0.007		
Juvenile					
Date	0.091	1	0.091	19.067	<0.001
Parasitism status	0.002	1	0.002	0.498	0.482
Sex	0.006	1	0.006	1.251	0.266
Habitat type	0.000	1	<0.001	0.074	0.786
Parasitism status*Sex	0.020	1	0.020	4.160	0.044
Parasitism status*Habitat type	<0.001	1	<0.001	0.002	0.967
Sex*Habitat type	<0.001	1	<0.001	0.000	0.990
Parasitism status*Sex*Habitat type	0.013	1	0.013	2.728	0.102
Error	0.474	99	0.005		

Table 4.3. Comparisons of mean body mass index ($\pm$ SE) of bot fly parasitized and nonparasitized adult and juvenile Ord's kangaroo rats.

	Adult		Juvenile	
	Female	Male	Female	Male
Overall				
Parasitized	0.003 $\pm$ 0.013	0.027 $\pm$ 0.011	-0.002 $\pm$ 0.021	0.052 $\pm$ 0.019
Nonparasitized	-0.013 $\pm$ 0.013	0.030 $\pm$ 0.009	0.014 $\pm$ 0.011	0.020 $\pm$ 0.014
Sand dune				
Parasitized	-0.001 $\pm$ 0.033	0.078 $\pm$ 0.021	-0.042 $\pm$ 0.038	0.090 $\pm$ 0.043
Nonparasitized	-0.002 $\pm$ 0.021	0.067 $\pm$ 0.018	0.024 $\pm$ 0.027	-0.049 $\pm$ 0.053
Road				
Parasitized	0.004 $\pm$ 0.015	0.018 $\pm$ 0.012	0.012 $\pm$ 0.023	0.044 $\pm$ 0.020
Nonparasitized	-0.014 $\pm$ 0.014	0.024 $\pm$ 0.010	0.012 $\pm$ 0.012	0.025 $\pm$ 0.015

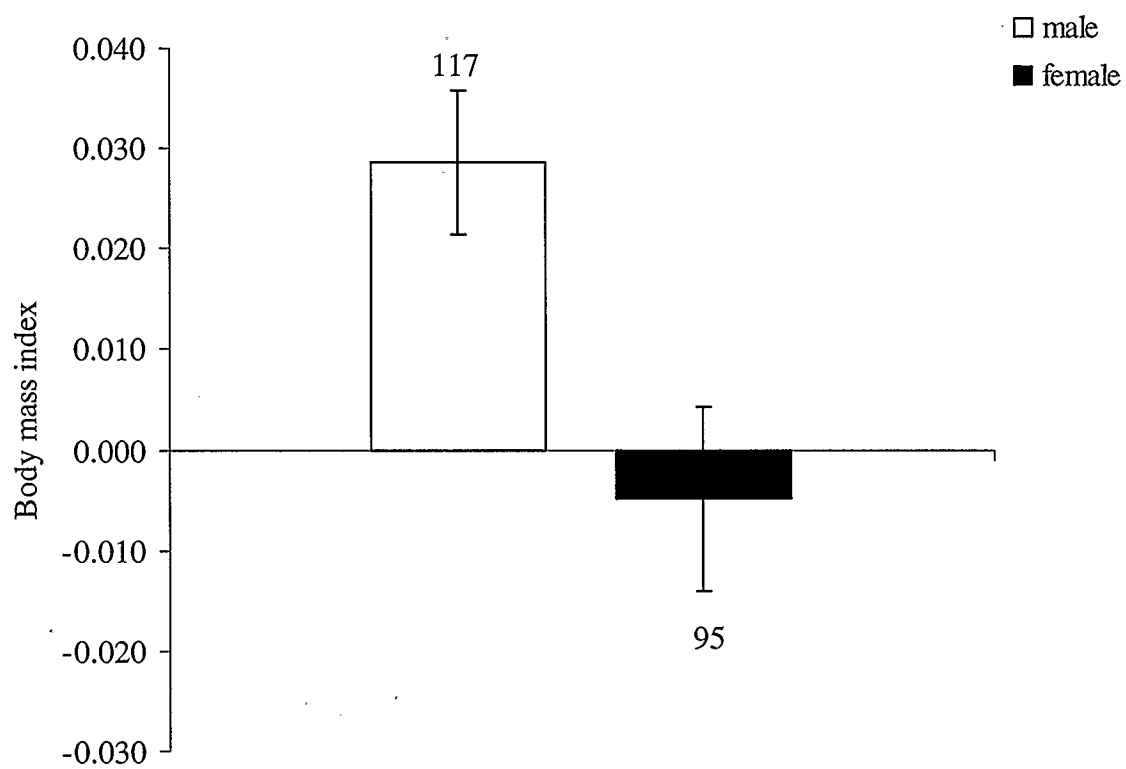


Figure 4.3. The mean body mass index for adult male and female Ord's kangaroo rat. Numbers outside the error bars indicate sample size.

(Table 4.2 and 4.3). However, the parasitism status and sex interaction term for juveniles was significant, such that the BMI of parasitized juvenile females was 26 times lower than parasitized males (Figure 4.4). The BMI of adult and juvenile kangaroo rats was not associated with the intensity of parasitism (Table 4.4).

Effects on Reproduction

Individual-level analysis

Female analysis

The majority of adult females were reproductively active during May, June, and July, and no reproductive activity was observed after August 24 (Figure 4.5a). Consequently, this analysis was restricted to kangaroo rat captures during the period when the bot fly and breeding season overlapped (i.e., July 12 to August 24). Forty-five out of 158 (28.5%) adult females were parasitized during this period. Of the reproductively active adult females, 13 out of 45 (28.9%) were parasitized, and 48 out of 113 (42.5%) were nonparasitized, but the difference was not significant ($\chi^2 = 2.51$, $df = 1$, $P = 0.11$). Fewer parasitized adult females were observed to be pregnant or lactating than nonparasitized adult females, although a similar proportion were observed to have lactated previously (Table 4.5). No parasitized females ($n = 12$) were observed to become reproductively active after their parasitism event.

There is limited anecdotal evidence that bot fly parasitism may have impaired pregnancy and weaning in adult female kangaroo rats. The only parasitized pregnant female to be recaptured had no signs of lactation on a subsequent capture, suggesting a failure to rear a litter. Furthermore, three females were observed to be pregnant before they were parasitized, yet none were observed to be lactating or post-lactating on their

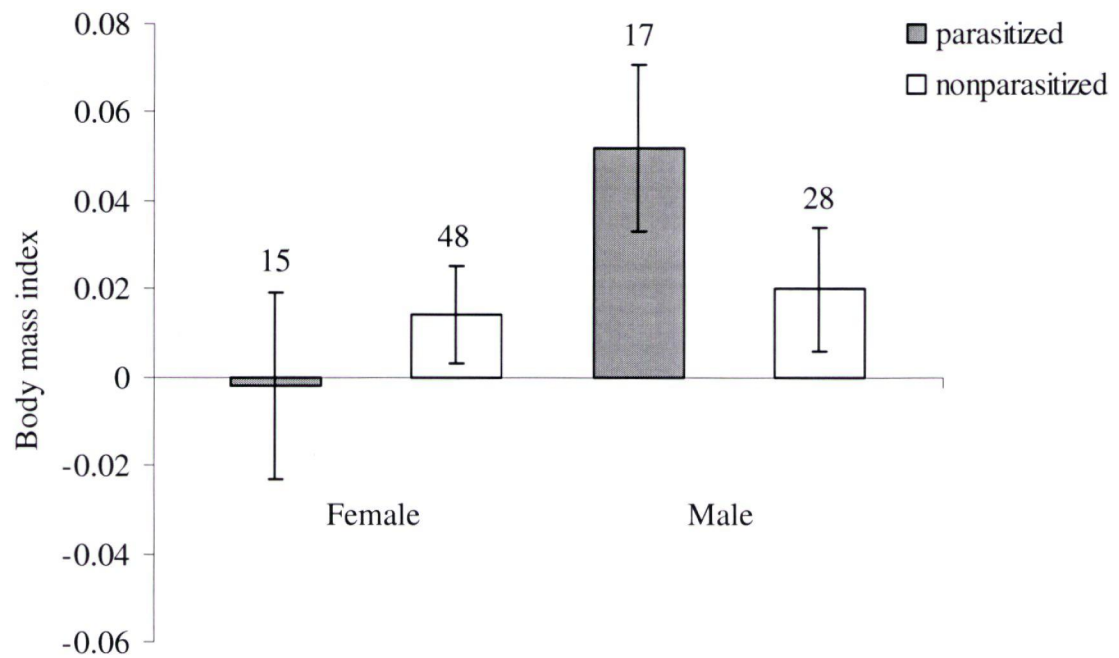
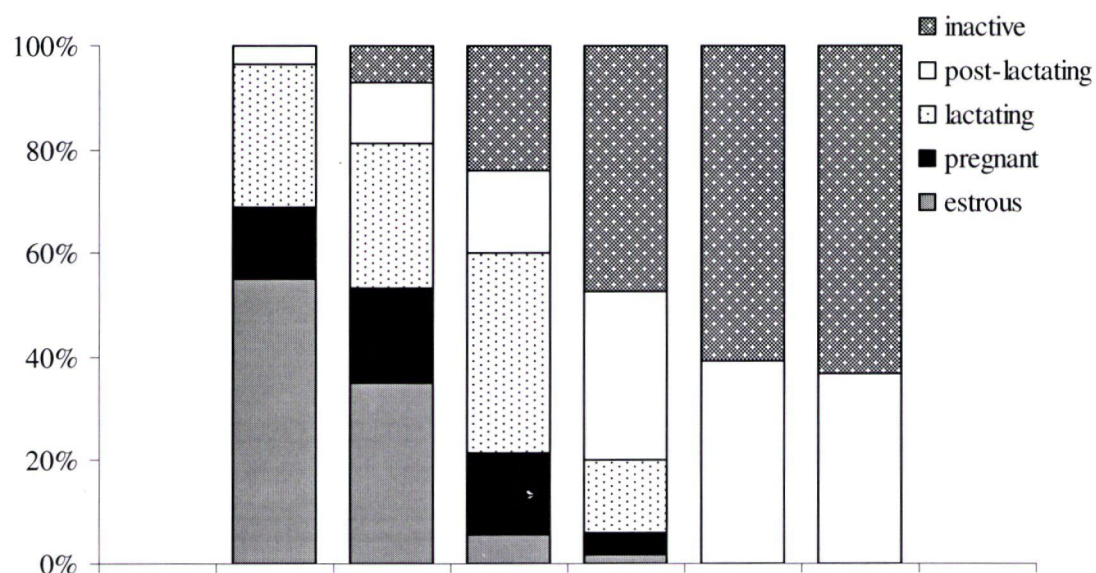


Figure 4.4 The body mass index of parasitized and nonparasitized juvenile female and male Ord's kangaroo rats. The only significant difference occurred between parasitized females and parasitized males. Numbers above the error bars indicate sample size.

Table 4.4. ANCOVA for the effects of the intensity of parasites, sex, and habitat type (sand dunes and roads) on the body mass index (BMI) of adult and juvenile Ord's kangaroo rats.

Source of variation	Sum of squares	Df	Mean square	F-ratio	P
Adult					
Intensity (covariate)	<0.001	1	<0.001	0.013	0.910
Date (covariate)	0.002	1	0.002	0.286	0.593
Sex	0.070	1	0.070	10.214	0.002
Habitat type	0.020	1	0.020	2.890	0.091
Sex*Habitat type	0.015	1	0.015	2.121	0.147
Error	1.413	206	0.007		
Juvenile					
Intensity (covariate)	0.009	1	0.009	1.907	0.170
Date (covariate)	0.108	1	0.108	22.507	0.000
Sex	0.005	1	0.005	0.937	0.335
Habitat type	0.003	1	0.003	0.603	0.439
Sex*Habitat type	<0.001	1	<0.001	0.000	0.987
Error	0.491	102	0.005		

a)



b)

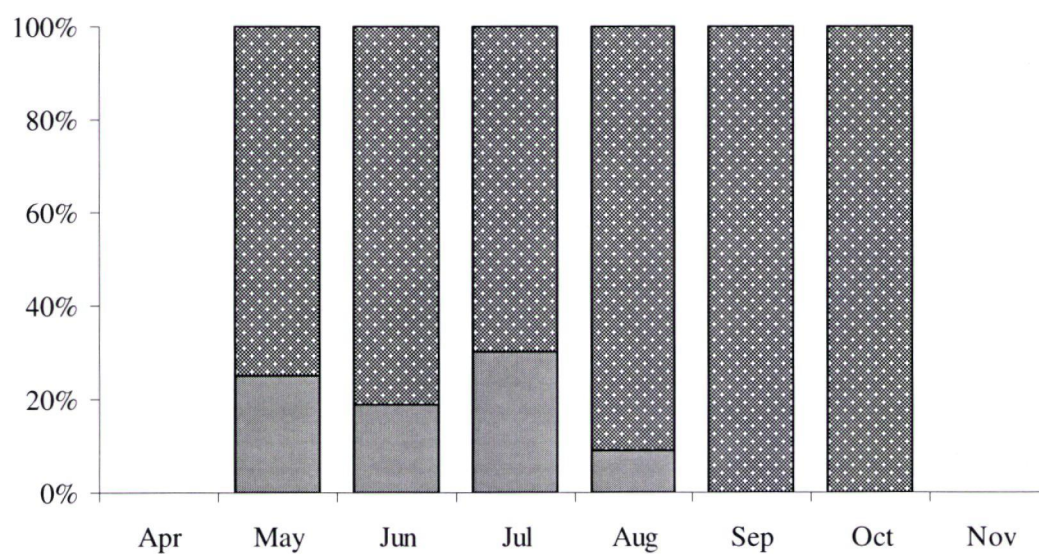


Figure 4.5. The percentage of adult (a) and juvenile (b) female Ord's kangaroo rats that were post-lactating, lactating, pregnant, estrous and reproductively not active for each month surveyed in 2004.

Table 4.5. The reproductive condition of parasitized and nonparasitized adult female Ord's kangaroo rats during the bot fly season. The reproductive condition of parasitized females was measured while the larvae was present or shortly after emergence.

	Reproductive condition					Total
	Estrous	Pregnant	Lactating	Post-lactating	Non	
Parasitized	4	2	7	20	12	45
Nonparasitized	4	16	28	23	42	113

next capture. Of seven parasitized females that were lactating, four of them had larvae positioned in the abdominal region, which may have interfered with the functioning of the teats. Conversely, successive captures (five in one month) of one of these females revealed that she was lactating, suggesting she may have successfully reared a litter while parasitized.

Results from the forward stepwise logistic regression showed that parasitism was not significantly associated with reproductive status, and no significant interactions existed between parasitism and habitat, BMI, or date (Table 4.6). The best model from the forward stepwise logistic regression analysis included only date as a significant predictor of reproductive status. For each day increase in date, the odds of an adult female being reproductively active were reduced (by a factor of 0.93). The result was the same when the intensity of parasites was used as a predictor of reproductive status; only date was retained in the final model (Table 4.6).

The number of juvenile females parasitized was 18 out of 74 (24.3%). The majority of juvenile females were not reproductively active, and the only reproductive condition observed was 'estrous' (Figure 4.5b). Approximately 27.8% of parasitized (5/18) and 14.3% of nonparasitized (8/56) juvenile females were estrous, although this difference was not significant (Fisher's Exact Test, $P = 0.29$).

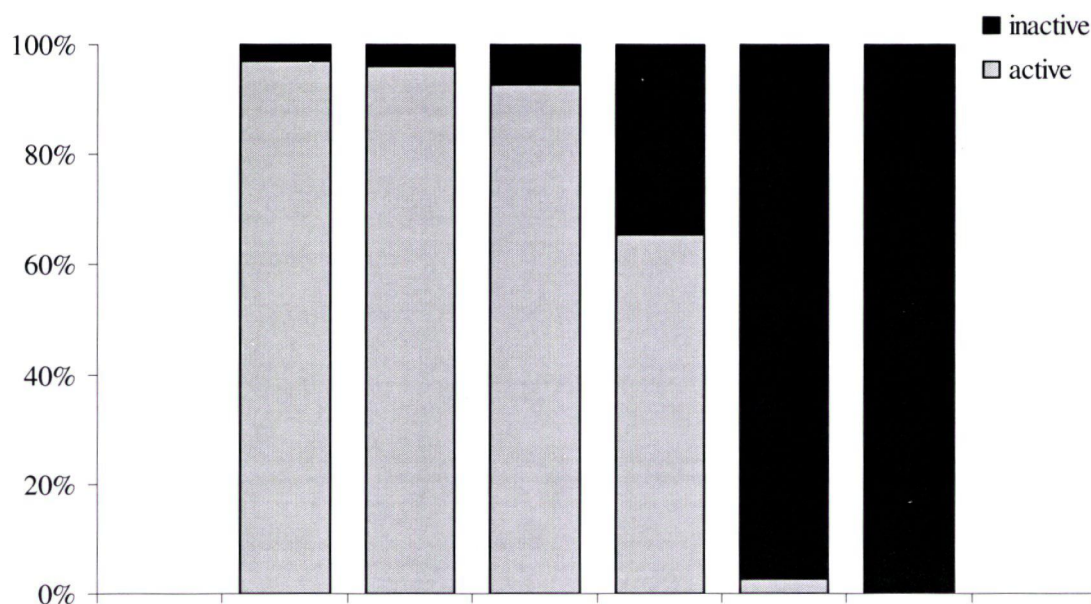
Male analysis

Adult males were reproductively active from May through to early September (Figure 4.6a). After September 6, only one of 90 males was observed to be reproductively active; I removed this record from the analysis. Thus, the timing for the male analysis

Table 4.6. Logistic regression model of the effects of parasitism status (and intensity), habitat type (river valley slope, sand dune, and road), body mass index (BMI), and date on the probability of being reproductively active for adult female Ord's kangaroo rats. A forward stepwise procedure with the log-likelihood ratio criterion was used.

Variables	β	SE	Wald's χ^2	P	Odds Ratio	95% CI
Parasitism status						
Variables in the equation						
Constant	15.80	3.20	24.39	<0.001		
Date	-0.08	0.02	26.28	<0.001	0.93	0.90-0.95
Variables not in the equation						
Parasitism status				0.430		
Habitat				0.197		
Dune				0.076		
Road				0.805		
BMI				0.077		
Parasitism status*Habitat				0.422		
Parasitism status*Dune				0.708		
Parasitism status*Road				0.236		
Parasitism status*BMI				0.936		
Parasitism status*Date				0.438		
Intensity						
Variables in the equation						
Constant	15.80	3.20	24.39	<0.001		
Date	-0.76	0.15	26.28	<0.001	0.93	0.90-0.95
Variables not in the equation						
Intensity				0.663		
Habitat				0.197		
Dune				0.076		
Road				0.663		
BMI				0.077		
Intensity*Habitat				0.807		
Intensity *Dune				0.762		
Intensity *Road				0.586		
Intensity *BMI				0.629		
Intensity *Date				0.686		

a)



b)

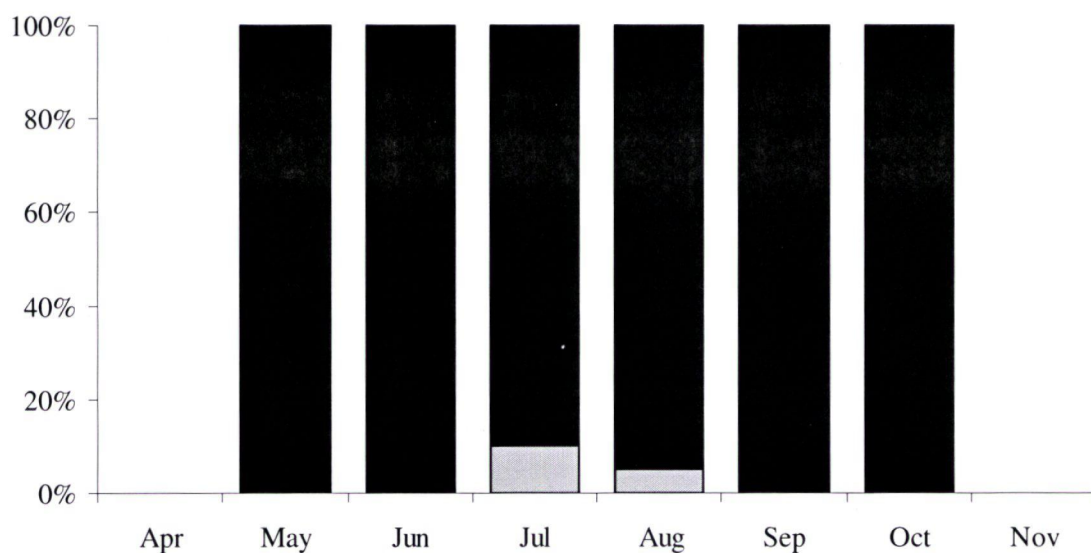


Figure 4.6. The percentage of adult (a) and juvenile (b) male Ord's kangaroo rats that were reproductively active and not active for each month surveyed in 2004.

was restricted to observations between July 12 and September 6, the period when male reproductive activity and the bot fly season overlapped. The number of adult males parasitized by bot fly larva during this time was 47 out of 179 (26.3%). There was no difference between the proportion of parasitized males (70.2%; 33/47) and nonparasitized males (75.8%; 100/132) that were reproductively active ($\chi^2 = 0.56$, $df = 1$, $P = 0.46$).

Results from the forward stepwise logistic regression showed that reproductive status was independent of parasitism status, as were interactions between parasitism and habitat, BMI, and date (Table 4.7). Only BMI was found to predict the reproductive status of adult males, while date was marginally significant (Table 4.7). Intensity was found to not be associated with reproductive status for adult males, even though the interaction between intensity and BMI was retained in the final model (Table 4.7). This indicates that more heavily parasitized adult males with a lower BMI are less likely to be reproductively active.

The number of juvenile males parasitized by bot fly larva was 12 out of 56 (21.4%). Juvenile males were only observed to be reproductively active during July and August (Figure 4.6b). No parasitized juvenile males were reproductively active. The number of nonparasitized juvenile males that were reproductively active was only 4 of 44 (9.1%).

Population-level analysis

I estimated that 86 juveniles were born shortly before or during the bot fly season. There was not a significant relationship between juvenile recruitment and bot fly prevalence at each site (Spearman rank correlation $r_s = -0.238$, $n = 8$, $P = 0.570$; Figure

Table 4.7. Logistic regression model of the effects of parasitism status (and intensity), habitat type (river valley slope, sand dune, and road), body mass index (BMI), and date on the probability of being reproductively active for adult male Ord's kangaroo rats. A forward stepwise procedure with the log-likelihood ratio criterion was used.

Variables	β	SE	Wald's χ^2	P	Odds Ratio	95% CI
Parasitism status						
Variables in the equation						
Constant	0.78	0.19	17.23	<0.001	2.17	
BMI	10.86	2.59	17.52	<0.001	51860	321-8.4e6
Variables not in the equation						
Parasitism status				0.671		
Habitat				0.350		
Dune				0.150		
Road				0.573		
Date				0.083		
Parasitism status*Habitat				0.872		
Parasitism status*Dune				0.932		
Parasitism status*Road				0.602		
Parasitism status*BMI				0.103		
Parasitism status*Date				0.678		
Intensity						
Variables in the equation						
Constant	0.73	0.19	14.92	<0.001	2.08	
BMI	14.02	3.19	19.35	<0.001	1231921	2382-6.4e8
Intensity*BMI	-4.45	2.30	3.74	0.053	0.01	0.00-1.06
Variables not in the equation						
Intensity				0.375		
Habitat				0.308		
Dune				0.127		
Road				0.533		
Date				0.117		
Intensity*Habitat				0.622		
Intensity*Dune				0.982		
Intensity*Road				0.330		
Intensity*Date				0.412		

4.7). However, if sites with negligible prevalence (i.e., the river valley sites, N3 and N4) are removed, the relationship becomes significant ($r_s = -0.886$, $n = 6$, $P = 0.019$). I believe it was reasonable to remove the river valley habitat from the analysis because these sites had significantly lower prevalence than the other sites. As a result, the low number of juvenile recruits at the river valley sites cannot be attributed to bot fly parasitism and other unknown mechanisms may be occurring here.

Effects on Survival

Individual-level analysis

Overall survival

Table 4.8 shows the percentage of parasitized and nonparasitized kangaroo rats that survived. The stepwise logistic regression analysis revealed that parasitism status was not an important predictor of overall survival for adult kangaroo rats, although a number of other variables were significant: habitat type, sex, and the last capture date of 2004 (Table 4.9). The odds of survival for kangaroo rats inhabiting sand dunes and roads were reduced by a factor of 0.29 and 0.45, respectively, compared to kangaroo rats inhabiting the river valleys (Table 4.9). The odds of survival increased by a factor of 1.86 for male kangaroo rats. Individuals known to be alive later in 2004 had greater odds of recapture in 2005; for every one day increase in date, the odds of survival increased by a factor of 1.02. The percent survival of parasitized and nonparasitized adult female and male kangaroo rats is shown in Figure 4.8. When the intensity of parasites was considered instead of parasitism status, intensity also was not associated with overall survival of adult kangaroo rats (Table 4.10).

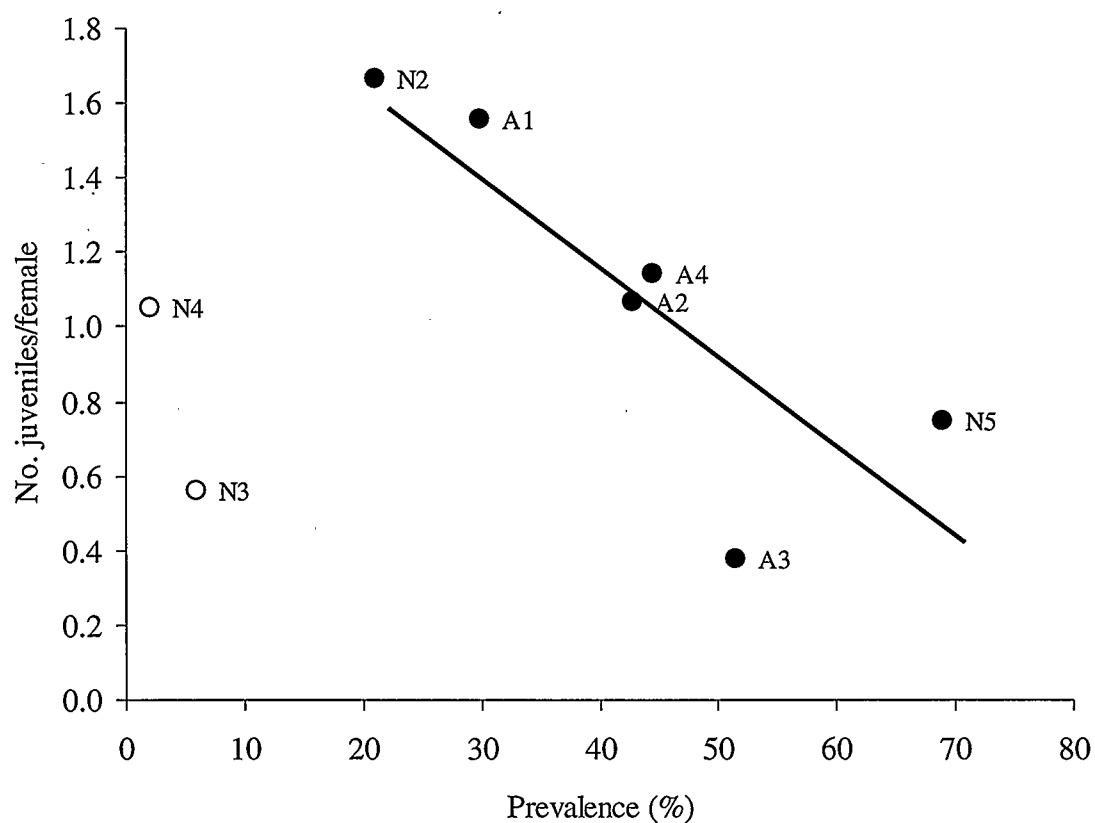


Figure 4.7. The number of juvenile Ord's kangaroo rats per breeding female as a function of bot fly prevalence at each study site. The study sites are identified by the labels on each point of measurement (see Figure 1.2). The treadline represents the significant relationship when sites N3 and N4 (i.e., the river valley sites, open circles) are removed.

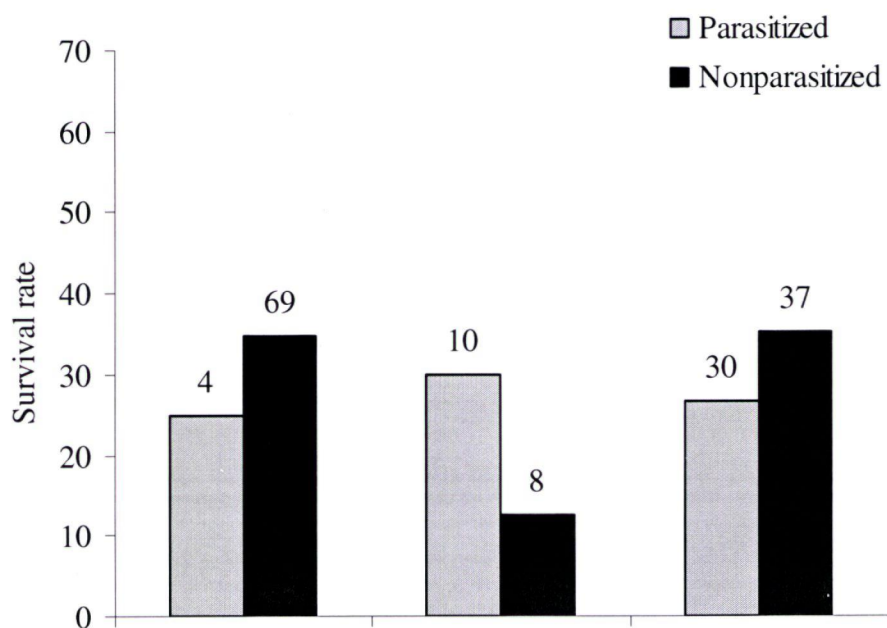
Table 4.8. Overall survival of parasitized and nonparasitized Ord's kangaroo rats in southeastern Alberta.

	Percent Surviving (n)						
	All individuals	All adults	Adult		All juveniles	Juvenile	
			male	female		male	female
Parasitized	29.6 (135)	34.7 (98)	42.3 (52)	27.3 (44)	16.7 (36)	13.3 (15)	26.7 (15)
Nonparasitized	34.4 (366)	39.7 (234)	46.2 (119)	33.3 (114)	24.8 (133)	32.7 (49)	25.4 (67)

Table 4.9. Logistic regression model of the effects of parasitism status, sex, habitat type (river valley, sand dune, and road), body mass index (BMI), and last 2004 capture date (Date) on the probability of survival for adult and juvenile Ord's kangaroo rats. A forward stepwise procedure with the log-likelihood ratio criterion was used.

Variables	β	SE	Wald's χ^2	P	Odds Ratio	95% CI
Adult						
Variables in the Equation						
Habitat			11.28	0.004		
Dune	-1.25	0.457	7.43	0.006	0.29	0.12 - 0.70
Road	-0.80	0.282	7.99	0.005	0.45	0.26 - 0.78
Sex	0.62	0.249	6.22	0.013	1.86	1.14 - 3.03
Date	0.02	0.005	10.84	0.001	1.02	1.01 - 1.03
Constant	-4.09	1.129	13.10	<0.001	0.02	
Variables not in the Equation						
Parasitism status				0.495		
BMI				0.645		
Parasitism status*Habitat				0.525		
Parasitism status*Dune				0.355		
Parasitism status*Road				0.509		
Parasitism status*Sex				0.572		
Parasitism status*BMI				0.399		
Juvenile						
Variables in the Equation						
Date	0.02	0.008	6.11	0.013	1.02	1.00 - 1.03
Constant	-5.55	1.844	9.05	0.003	0.00	
Variables not in the Equation						
Parasitism status				0.224		
Habitat				0.489		
Dune				0.982		
Road				0.283		
Sex				0.808		
BMI				0.605		
Parasitism status*Habitat				0.515		
Parasitism status*Dune				0.558		
Parasitism status*Road				0.347		
Parasitism status*Sex				0.187		
Parasitism status*BMI				0.874		

(a)



(b)

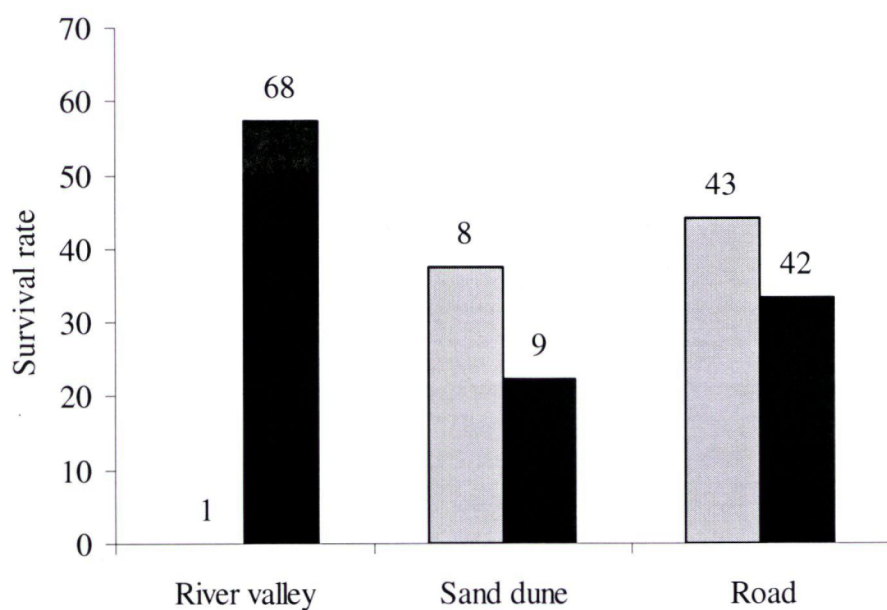


Figure 4.8. Overall survival (%) of adult female (a) and male (b) Ord's kangaroo rats at the river valley, sand dune, and road habitat types.

Table 4.10 Logistic regression model of the effects of intensity, sex, habitat type (river valley, sand dune, and road), body mass index (BMI), and last 2004 capture date (Date) on the probability of survival for adult and juvenile Ord's kangaroo rats. A forward stepwise procedure with the log-likelihood ratio criterion was used.

Variables	β	SE	Wald's χ^2	P	Odds Ratio	95% CI
Adult						
Variables in the Equation						
Habitat			11.28	0.004		
Dune	-1.25	0.457	7.43	0.006	0.29	0.12 -0.70
Road	-0.80	0.282	7.99	0.005	0.45	0.26 -0.78
Sex	0.62	0.249	6.22	0.013	1.86	1.14 -3.03
Date	0.02	0.005	10.84	0.001	1.02	1.01 -1.03
Constant	-4.09	1.129	13.10	<0.001	0.02	
Variables not in the Equation						
Intensity				0.863		
BMI				0.645		
Intensity*Habitat				0.175		
Intensity*Dune				0.078		
Intensity*Road				0.549		
Intensity*Sex				0.874		
Intensity*BMI				0.502		
Juvenile						
Variables in the Equation						
Date	0.02	0.008	6.11	0.013	1.02	1.00 -1.03
Constant	-5.55	1.844	9.05	0.003	0.00	
Variables not in the Equation						
Intensity				0.820		
Habitat				0.489		
Dune				0.982		
Road				0.283		
Sex				0.808		
BMI				0.605		
Intensity*Habitat				0.978		
Intensity*Dune				0.852		
Intensity*Road				0.932		
Intensity*Sex				0.561		
Intensity*BMI				0.595		

Parasitism status was also not a predictor of overall survival for juvenile kangaroo rats (Table 4.9). Interactions between parasitism status and habitat, parasitism status and BMI, and parasitism status and sex were not significant predictors of survival (Figure 4.9; Table 4.9). The final model only included the last capture date of 2004 as a significant predictor of overall survival. The odds of survival increased for every one day increase in date (by a factor of 1.02). As well, when intensity was used instead of parasitism status, intensity was not a significant predictor of overall survival for juvenile kangaroo rats (Table 4.10).

Over-winter survival

Of adult kangaroo rats that survived the winter, 41.9% (18/43) were parasitized and 35.8% (19/53) were nonparasitized. Neither parasitism status nor any interactions with parasitism were retained in the final logistic regression model for adult kangaroo rats (Table 4.11). The intensity of parasites also did not influence over-winter survival of adult kangaroo rats (Table 4.11). The result also did not differ for juveniles, 28.6% (2/7) of parasitized and 36.4% (12/33) of nonparasitized juvenile kangaroo rats survived the winter (Fisher's Exact test, $P = 1.00$).

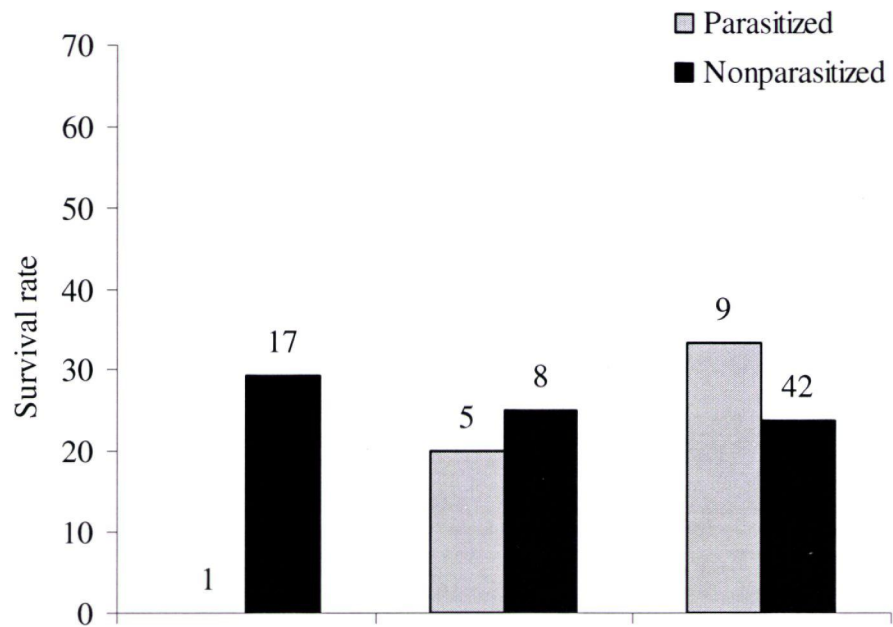
Population-level analysis

Adult survival

The adult data provided a reasonably good fit to the global model. The median $\hat{c}$ value was 1.34, suggesting the presence of some overdispersion. This value of $\hat{c}$ was used to adjust all QAICc values in the adult analysis.

First, I modeled the recapture parameters. An additive model with habitat type, parasitism status, and time ($ph+i+t$; Table 4.12) was the best model to describe recapture

(a)



(b)

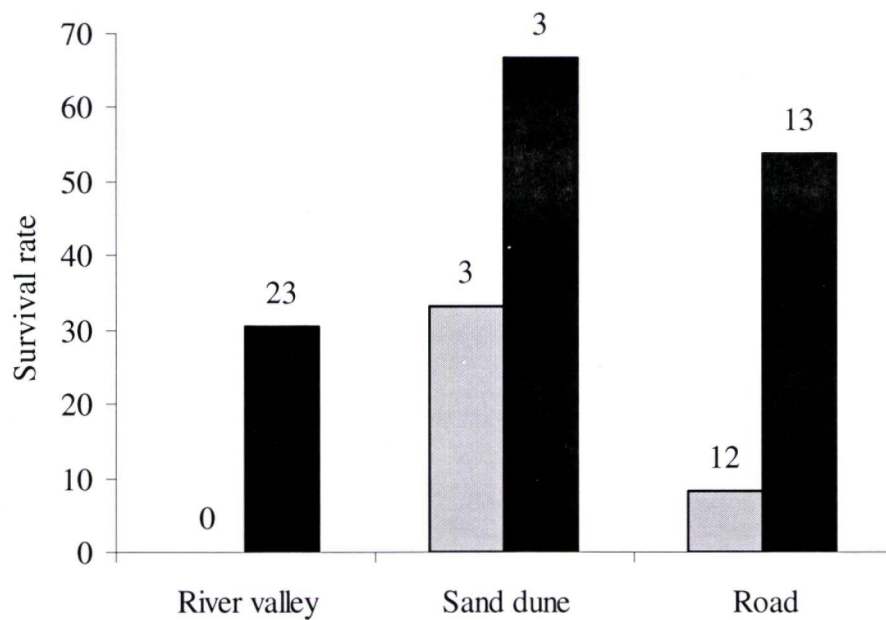


Figure 4.9. Overall survival (%) of juvenile female (a) and male (b) Ord's kangaroo rats at the river valley, sand dune, and road habitat types.

Table 4.11. Logistic regression model of the effects of parasitism status (and intensity), sex, and body mass index (BMI) on the probability of over-winter survival for adult Ord's kangaroo rats. A forward stepwise procedure with the log-likelihood ratio criterion was used.

Variables	β	SE	Wald	P	OR
Parasitism Status					
Variables in the Equation					
Constant	-0.467	0.210	4.951	0.026	0.627
Variables not in the Equation					
Parasitism status				0.547	
Sex				0.355	
BMI				0.235	
Parasitism status*Sex				0.294	
Parasitism status*BMI				0.718	
Intensity					
Variables in the Equation					
Constant	-0.467	0.210	4.951	0.026	0.627
Variables not in the Equation					
Intensity				0.308	
Sex				0.355	
BMI				0.235	
Intensity*Sex				0.948	
Intensity*BMI				0.437	

Table 4.12. Models describing factors affecting recapture rates of adult Ord's kangaroo rats using Program MARK. Recapture was modeled first to determine the best factors affecting recapture rates of adult kangaroo rats. Models were evaluated using Akaike's information criteria adjusted for sample size and overdispersion (QAICc).

Model	QAICc	Δ QAICc	Weight	N.P.	Dev.
1 $\Phi(h*i*s*t) p(h+i+t)$	1625.10	0	0.30	40	317.58
2 $\Phi(h*i*s*t) p(h+s+t)$	1625.62	0.52	0.23	40	318.10
3 $\Phi(h*i*s*t) p(i+t)$	1626.60	1.51	0.14	39	321.26
4 $\Phi(h*i*s*t) p(t)$	1626.99	1.89	0.12	39	321.65
5 $\Phi(h*i*s*t) p(h+t)$	1627.92	2.82	0.07	41	318.22
6 $\Phi(h*i*s*t) p(i+s+t)$	1628.77	3.67	0.05	40	321.25
7 $\Phi(h*i*s*t) p(s+t)$	1629.11	4.02	0.04	40	321.60
8 $\Phi(h*i*s*t) p(h+i+s+t)$	1629.40	4.30	0.04	42	317.52
9 $\Phi(h*i*s*t) p(s*t)$	1635.26	10.17	0.00	43	321.19
10 $\Phi(h*i*s*t) p(i*t)$	1635.61	10.51	0.00	44	319.34
11 $\Phi(h*i*s*t) p(h*t)$	1637.93	12.84	0.00	48	312.84
12 $\Phi(h*i*s*t) p(h*s*t)$	1638.71	13.61	0.00	52	304.71
13 $\Phi(h*i*s*t) p(h*i*t)$	1639.30	14.21	0.00	52	305.30
14 $\Phi(h*i*s*t) p(h)$	1648.01	22.91	0.00	33	355.62
15 $\Phi(h*i*s*t) p(i*s*t)$	1648.18	23.08	0.00	53	311.94
16 $\Phi(h*i*s*t) p(h*i*s*t)$	1653.68	28.59	0.00	66	287.90
17 $\Phi(h*i*s*t) p(.)$	1655.49	30.39	0.00	34	360.96
18 $\Phi(h*i*s*t) p(i)$	1657.22	32.13	0.00	35	360.54
19 $\Phi(h*i*s*t) p(s)$	1657.59	32.49	0.00	35	360.90

Φ = survival, p = recapture, h = habitat, i = parasitism status, s = sex, and t = time

QAICc = Quasi Akaike's information criterion, Δ QAICc = differences in QAIC, Weight = Akaike's weight, N.P. = number of parameters, and Dev. = deviance

probabilities of adult kangaroo rats. This parameterization was used in building subsequent survival models. Other models in the set were also likely, but I decided to use only the best model based on ΔQAICc and the Akaike weight. Based on the best model ($\Phi h * i * s * t, ph + i + t$), recapture rates were higher at sand dunes compared to roads, and within habitat recapture rates were higher for parasitized compared to nonparasitized kangaroo rats (Table 4.13).

The best model in the candidate model set for adult survival included time dependence only ($\Phi t, ph + i + t$; Table 4.14). Models 2, 3, and 4 also ranked highly based on the ΔQAICc and Akaike weight (Table 4.14). However, survival rates were not significantly different for any of these models based on the 95% confidence intervals of the coefficients (Cooch and White 2005; see Table 4.15). Model 2 ($\Phi h + t, ph + i + t$) compares survival between sand dune and road habitats, the beta parameter was 0.269 ± 0.241 (95% CI, -0.204 to 0.742). Model 3 ($\Phi i + t, ph + i + t$) compares survival between parasitized and nonparasitized individuals, the beta parameter was 0.245 ± 0.234 (95% CI, -0.703 to 0.213). Model 4 ($\Phi s + t, ph + i + t$) compares survival between males and females, the beta parameter was 0.131 ± 0.221 (95% CI, -0.303 to 0.565). The over-winter survival rates for the four best models are shown in Table 4.15.

Juvenile survival

The juvenile data provided a good fit to the global model. The median $\hat{c}$ value was 1.11; this value of $\hat{c}$ was used to adjust all QAICc values in the juvenile data analysis.

Again, I modeled recapture rates first. The best model describing recapture rates of juvenile kangaroo rats was an additive model with sex and time ($\Phi h * i * s * t, ps + t$; Table

Table 4.13. Mean recapture rates ($\pm$ SE) of parasitized and nonparasitized adult Ord's kangaroo rats at the road and sand dune habitat types, based on the best model ($\Phi(h*i*s*t) p(h+i+t)$). Recapture rates were higher at sand dunes compared to roads, and within habitat recapture rates were higher for parasitized kangaroo rats.

	Time interval				
	Jul-Aug	Aug-Sep	Sep-Oct	*Oct-May	May-Jun
Road					
Parasitized	0.639 $\pm$ 0.058	0.508 $\pm$ 0.052	0.280 $\pm$ 0.046	0.558 $\pm$ 0.060	0.670 $\pm$ 0.066
Nonparasitized	0.593 $\pm$ 0.071	0.460 $\pm$ 0.063	0.243 $\pm$ 0.049	0.510 $\pm$ 0.070	0.626 $\pm$ 0.078
Sand Dune					
Parasitized	0.740 $\pm$ 0.063	0.624 $\pm$ 0.067	0.385 $\pm$ 0.074	0.670 $\pm$ 0.073	0.766 $\pm$ 0.065
Nonparasitized	0.701 $\pm$ 0.076	0.578 $\pm$ 0.078	0.340 $\pm$ 0.077	0.626 $\pm$ 0.084	0.729 $\pm$ 0.078

* Over-winter interval

Table 4.14. Model selection of survival rates for adult Ord's kangaroo rats using Program MARK. Models are ranked according to the QAICc.

Model	QAICc	Δ QAICc	Weight	N.P.	Dev.
1 $\Phi(t) p(h+i+t)$	1646.15	0	0.27	13	363.78
2 $\Phi(h+t) p(h+i+t)$	1646.99	0.84	0.18	14	362.56
3 $\Phi(i+t) p(h+i+t)$	1647.06	0.91	0.17	14	362.63
4 $\Phi(s+t) p(h+i+t)$	1647.86	1.71	0.11	14	363.43
5 $\Phi(i+s+t) p(h+i+t)$	1648.24	2.09	0.09	15	361.75
6 $\Phi(h+s+t) p(h+i+t)$	1648.78	2.63	0.07	15	362.28
7 $\Phi(h+i+s+t) p(h+i+t)$	1649.29	3.14	0.06	16	360.73
8 $\Phi(h+i+t) p(h+i+t)$	1650.02	3.87	0.04	16	361.45
9 $\Phi(h*i*t) p(h+i+t)$	1654.77	8.62	0.00	26	345.28
10 $\Phi(s*t) p(h+i+t)$	1655.14	8.99	0.00	18	362.42
11 $\Phi(.) p(h+i+t)$	1655.70	9.54	0.00	9	381.51
12 $\Phi(h*t) p(h+i+t)$	1656.18	10.03	0.00	19	361.39
13 $\Phi(i) p(h+i+t)$	1656.72	10.57	0.00	10	380.49
14 $\Phi(h) p(h+i+t)$	1656.93	10.78	0.00	10	380.71
15 $\Phi(s) p(h+i+t)$	1657.51	11.36	0.00	10	381.28
16 $\Phi(i*t) p(h+i+t)$	1658.77	12.62	0.00	20	361.89
17 $\Phi(i*s*t) p(h+i+t)$	1665.02	18.87	0.00	29	349.18
18 $\Phi(h*i*s*t) p(h+i+t)$	1665.42	19.27	0.00	40	325.89
19 $\Phi(h*s*t) p(h+i+t)$	1665.96	19.81	0.00	29	350.12
20 $\Phi(h*i*s*t) p(h*i*s*t)$	1693.22	47.07	0.00	66	295.43

Φ = survival, p = recapture, h = habitat, i = parasitism status, s = sex, and t = time

QAICc = Quasi Akaike's information criterion, Δ QAICc = differences in QAIC, Weight = Akaike's weight, N.P.= number of parameters, and Dev. = deviance

Table 4.15. Over-winter survival estimates for the top four models in the candidate model set for adult Ord's kangaroo rats.

	Estimate	SE	95% Confidence Interval	
			Lower	Upper
Model 1 ($\Phi_t, ph+i+t$)	0.648	0.081	0.478	0.787
Model 2 ($\Phi_{h+t}, ph+i+t$)				
Road habitat	0.661	0.081	0.490	0.798
Sand dune habitat	0.598	0.098	0.402	0.767
Model 3 ($\Phi_{i+t}, ph+i+t$)				
Parasitized kangaroo rats	0.633	0.084	0.458	0.778
Nonparasitized kangaroo rats	0.687	0.085	0.503	0.827
Model 4 ($\Phi_{s+t}, ph+i+t$)				
Female kangaroo rats	0.653	0.081	0.483	0.791
Male kangaroo rats	0.622	0.094	0.429	0.783

4.16). This parameterization was used in building subsequent survival models. Model ($\Phi h * i * s * t, ps + t$) was 2.6 times better supported by the data compared to the second best model. Based on the top model, female recapture rates were higher than male (Table 4.17).

Similar to the adults, the best model included time dependence only ($\Phi t, ps + t$; Table 4.18). This model was 2.7 times more likely than the next best model, Model 2 ($\Phi h + t, ps + t$), which included habitat and time dependence. Models 3 and 4 also ranked high. Once more, survival rates were not significantly different for any of these models. Model 2 ($\Phi h + t, ps + t$) compares survival between sand dune and road habitats, the beta parameter was 0.106 ± 0.267 (95% CI, -0.630 to 0.417). Model 3 ($\Phi s + t, ps + t$) compares survival between females and males; the beta parameter was 0.042 ± 0.240 (95% CI, -0.513 to 0.429). Model 4 ($\Phi i + t, ps + t$) compares survival between parasitized and nonparasitized individuals, the beta parameter was 0.102 ± 0.278 (95% CI, -0.443 to 0.648). The over-winter survival rates for the four best models are shown in Table 4.19.

Effects on movement

The average MRD was 41.09 ± 5.48 m and 42.96 ± 5.54 m for parasitized and nonparasitized kangaroo rats, respectively, and were not significantly different ($t = -0.215$, $df = 126$, $P = 0.830$). Also, the distributions of the MRD were not different between parasitized and nonparasitized individuals (Kolmogorov-Smirnoff test, $D = 0.13$, $P = 0.71$).

Table 4.16. Model selection results for recapture models of the juvenile Ord's kangaroo rat data set using Program MARK. Recapture was modeled first to determine the best factors affecting recapture rates of juveniles. Models were evaluated using Akaike's information criteria adjusted for sample size and overdispersion (QAICc).

Model	QAICc	Δ QAICc	Weight	N.P.	Dev.
1 $\Phi(h*i*s*t) p(s+t)$	847.49	0.00	0.57	29	216.55
2 $\Phi(h*i*s*t) p(h+s+t)$	849.42	1.93	0.22	31	213.87
3 $\Phi(h*i*s*t) p(h+t)$	851.65	4.16	0.07	32	213.77
4 $\Phi(h*i*s*t) p(t)$	852.02	4.53	0.06	31	216.46
5 $\Phi(h*i*s*t) p(h+i+t)$	853.93	6.44	0.02	33	213.72
6 $\Phi(h*i*s*t) p(i+t)$	854.03	6.53	0.02	32	216.15
7 $\Phi(h*i*s*t) p(i*t)$	854.76	7.26	0.02	34	212.20
8 $\Phi(h*i*s*t) p(i+s+t)$	856.08	8.59	0.01	33	215.87
9 $\Phi(h*i*s*t) p(h*t)$	856.11	8.62	0.01	35	211.21
10 $\Phi(h*i*s*t) p(h*i*s*t)$	857.71	10.21	0.00	47	183.63
11 $\Phi(h*i*s*t) p(h+i+s+t)$	858.06	10.57	0.00	35	213.16
12 $\Phi(h*i*s*t) p(h*s*t)$	858.40	10.90	0.00	40	201.54
13 $\Phi(h*i*s*t) p(h*i*t)$	858.92	11.43	0.00	41	199.64
14 $\Phi(h*i*s*t) p(h)$	860.02	12.52	0.00	24	240.40
15 $\Phi(h*i*s*t) p(.)$	862.36	14.87	0.00	23	244.98
16 $\Phi(h*i*s*t) p(i*s*t)$	863.02	15.52	0.00	40	206.16
17 $\Phi(h*i*s*t) p(i)$	863.95	16.46	0.00	24	244.34
18 $\Phi(h*i*s*t) p(s)$	864.54	17.05	0.00	24	244.92
19 $\Phi(h*i*s*t) p(s*t)$	865.75	18.25	0.00	37	216.10

Φ = survival, p = recapture, h = habitat, i = parasitism status, s = sex, and t = time

QAICc = Quasi Akaike's information criterion, Δ QAICc = differences in QAIC, Weight = Akaike's weight, N.P. = number of parameters, and Dev. = deviance

Table 4.17. Mean recapture rates ($\pm$ SE) based on the best model ($\Phi h^* i^* s^* t$, $p s + t$) from the candidate model set for juvenile Ord's kangaroo rats at the road and sand dune habitat types. Note that the recapture rate for the final interval cannot be estimated.

	Time interval				
	Jul-Aug	Aug-Sep	Sep-Oct	*Oct-May	May-Jun
Female	0.387 $\pm$ 0.060	0.378 $\pm$ 0.071	0.217 $\pm$ 0.061	0.714 $\pm$ 0.078	0.600 $\pm$ 0.091
Male	0.367 $\pm$ 0.081	0.359 $\pm$ 0.081	0.203 $\pm$ 0.066	0.696 $\pm$ 0.090	0.580 $\pm$ 0.090

* Over-winter interval

Table 4.18. Model selection of survival rates for juvenile Ord's kangaroo rats using Program MARK. Models are in ascending order according to QAICc.

Model	QAICc	Δ QAICc	Weight	N.P.	Dev.
1 $\Phi(t) p(s+t)$	837.04	0.00	0.38	11	245.66
2 $\Phi(h+t) p(s+t)$	838.99	1.95	0.14	12	245.50
3 $\Phi(s+t) p(s+t)$	839.12	2.08	0.13	12	245.63
4 $\Phi(i+t) p(s+t)$	839.13	2.08	0.13	12	245.63
5 $\Phi(i+s+t) p(s+t)$	840.86	3.82	0.06	13	245.25
6 $\Phi(h+i+t) p(s+t)$	841.02	3.98	0.05	13	245.40
7 $\Phi(h+s+t) p(s+t)$	841.09	4.05	0.05	13	245.48
8 $\Phi(h+i+s+t) p(s+t)$	842.87	5.82	0.02	14	245.12
9 $\Phi(h^*t) p(s+t)$	844.10	7.06	0.01	15	244.21
10 $\Phi(s^*t) p(s+t)$	844.61	7.57	0.01	15	244.72
11 $\Phi(i^*t) p(s+t)$	845.19	8.15	0.01	16	243.15
12 $\Phi(h^*i^*s^*t) p(s+t)$	847.49	10.45	0.00	29	216.55
13 $\Phi(i^*s^*t) p(s+t)$	848.05	11.01	0.00	21	235.10
14 $\Phi(.) p(s+t)$	849.41	12.37	0.00	8	264.30
15 $\Phi(h) p(s+t)$	851.34	14.30	0.00	9	264.15
16 $\Phi(i) p(s+t)$	851.43	14.39	0.00	9	264.24
17 $\Phi(s) p(s+t)$	851.48	14.44	0.00	9	264.29
18 $\Phi(h^*s^*t) p(s+t)$	856.50	19.46	0.00	25	234.63
19 $\Phi(h^*i^*s^*t) p(h^*i^*s^*t)$	857.71	20.67	0.00	47	183.63
20 $\Phi(h^*i^*t) p(s+t)$	858.48	21.43	0.00	25	236.61

Φ = survival, p = recapture, h = habitat, i = parasitism status, s = sex, and t = time

QAICc = Quasi Akaike's information criterion, Δ QAICc = differences in QAIC, Weight = Akaike's weight, N.P. = number of parameters, and Dev. = deviance

Table 4.19. Over-winter survival estimates for the top four models in the candidate model set for juvenile Ord's kangaroo rats.

	Estimate	SE	95% Confidence Interval	
			Lower	Upper
Model 1 ($\Phi_t, ps+t$)	0.523	0.110	0.316	0.722
Model 2 ($\Phi_{h+t}, ps+t$)				
Road habitat	0.544	0.121	0.315	0.756
Sand dune habitat	0.518	0.111	0.311	0.719
Model 3 ($\Phi_{s+t}, ps+t$)				
Female kangaroo rats	0.519	0.112	0.310	0.722
Male kangaroo rats	0.530	0.116	0.311	0.738
Model 4 ($\Phi_{i+t}, ps+t$)				
Parasitized kangaroo rats	0.532	0.111	0.321	0.731
Nonparasitized kangaroo rats	0.510	0.119	0.287	0.723

DISCUSSION

Effects on Body Condition

I hypothesized that parasitized kangaroo rats would experience significant weight loss because they are an atypical host for *C. polita*. However, my hypothesis was not supported; parasitized kangaroo rats did not have a lower body mass index than nonparasitized kangaroo rats. In native hosts, parasitism appears to have little effect on the body mass of the host. Munger and Karasov (1994) determined that bot fly parasitism has little impact on the energy budget of the host. They found that a single bot fly larva consumes only about 1% of the energy intake of the host. Additionally, bot fly larvae did not affect the digestive efficiency of the host (Munger and Karasov 1994).

Alternatively, parasitized kangaroo rats may have increased their food intake to compensate for the energetic costs of parasitism. Since kangaroo rats store seeds, they would presumably have access to sufficient quantities of food during the infection period. In laboratory studies, parasitized deer mice consumed more food during the final stages of parasitism and continued to do so for several days after the larvae vacated (Hunter and Webster 1974). Conversely, Munger and Karasov (1994) did not observe an increase in the food intake of parasitized white-footed mice in the laboratory, but they suggest that infected animals in the field increase their food intake to compensate for the costs of bot fly parasitism.

Previous studies have reported that individuals with a high intensity of parasites experience considerable weight loss (Baird 1972, Bennett 1973, Catts 1982). I did not find a negative effect of parasite intensity on the body condition of adult or juvenile

kangaroo rats, although some individuals with heavy burdens did seem to be emaciated and in poor condition.

Effects on Reproduction

Individual-level analysis

Contrary to my hypothesis, there was not a difference in the proportion of parasitized and nonparasitized kangaroo rats that were reproductively active, for either sex or age group. Apparently, the energetic costs of bot fly parasitism did not induce adult kangaroo rats into a non-reproductive condition. As well, parasitized juvenile kangaroo rats did not appear to delay sexual maturity.

The results from the female analysis in this study contradict previous studies, where female animals parasitized by bot flies were in a non-reproductive state more often than nonparasitized females (*M. pennsylvanicus*, Clough 1965, Iverson and Turner 1968; *P. boylii*, Hensley 1976; *M. townsendii*, Boonstra et al. 1980). My results support the findings of Getz (1970), Munger and Karasov (1991), and Burns et al. (2005), which found that bot fly parasitism did not significantly reduce breeding activity in adult females.

Negative effects on the reproductive condition of female kangaroo rats may not have been detected because the peak of the female breeding season occurred in May and June, while the peak of the bot fly season did not occur until August. Consequently, the majority of adult females had completed their breeding activity, and, based on the capture records, many parasitized females appeared to have given birth and weaned offspring prior to becoming parasitized. For this reason, the impact of bot fly parasitism on female reproduction may not have been revealed.

The period of bot fly parasitism may vary from year to year and environmental conditions most likely influence pupal development (Dunaway et al. 1967, Hunter et al. 1972, Catts 1982, Clark and Kaufman 1990). For example, Dunaway et al. (1967) suggest that an early spring or a late spring would presumably accelerate or delay emergence and cold weather events may abbreviate the parasitism season by killing adult flies. In previous years, the bot fly season in Alberta has started as early as mid June, thus, there is potential for greater overlap between the parasitism season and kangaroo rat breeding (Gummer et al. 1997). If the bot fly season coincides with the peak of the kangaroo rat's breeding season, I speculate that parasitism may decrease reproductive activity in parasitized females.

I also did not detect a decrease in reproductive activity of parasitized males, supporting the findings of Getz (1970) and Munger and Karasov (1991). Usually, the inguinal location of bots in male animals is the reason why parasitized individuals are not reproductively active. In this study, the majority of male kangaroo rats did not have bots located in the inguinal region. Only 3 of 47 infected males had larvae located near their testes. This differs from the findings of Dalmat (1943), Wecker (1962), and Dunaway et al. (1967) for white-footed mice. Bot fly species tend to be specific to a location on the body of the host, and many species are found in the inguinal region of the host (e.g., *C. emasculator* and *C. fontinella*). However, *C. polita* is rarely reported to be located in the inguinal region of the host (Richens 1965, Graham and Capelle 1970, Gummer et al. 1997).

The results of the intensity analysis for adult males showed that as the intensity of parasites increased and BMI decreased, the odds of being reproductively active were

reduced. Yet, out of the most heavily parasitized males, 63% were reproductively active. It appears that reproductive activity was related more to the BMI than intensity.

Population-level analysis

I found a significant negative correlation between juvenile recruitment and study sites with high bot fly prevalence. This result seems contradictory to the individual-level analysis where a significant reduction in reproductive activity of parasitized adult kangaroo rats was not detected. Parasitized kangaroo rats may have displayed signs of reproductive activity as often as nonparasitized kangaroo rats. Nevertheless, juvenile recruitment could still have been affected because of the energetic costs and physical hindrance of the larvae which may have inhibited copulation, pregnancy, or successful weaning of young. Anecdotal evidence showed that parasitized female kangaroo rats captured while pregnant or lactating did not successfully rear young, although the sample size was small. In addition, Sillman (1955) reported that infected females successfully gave birth, but the litters were not successfully reared. Smith (1977b) reported that infected female deer mice became pregnant but reabsorbed the embryos. Conversely, Timm and Cook (1979) found no significant difference in the number of embryos, corpora lutea, or placental scars between infected and noninfected white-footed mice, and unexpectedly found that parasitized females had greater uterine productivity. They did not examine birth rates or rearing of young.

My measure of juvenile recruitment was a rather coarse estimate. I assumed that the number of juveniles captured reflects the number of juveniles that were actually recruited into the population. I believe this assumption was reasonable because juvenile kangaroo rats tend to remain on or adjacent to their natal home (Jones 1993, Gummer

1997a). Thus, my estimate of juvenile recruitment should be a useful measure. The actual effects of parasitism on the successful rearing and survival of young were not determined in this study, however, and further investigation is necessary. A more direct measure of reproductive success between parasitized and nonparasitized females should be conducted to substantiate the results of this study.

I removed the river valley sites from the analysis because they had significantly lower prevalence than the other sites and appeared to be outlying data points. The low number of juveniles at these sites did not appear to be caused by parasitism and therefore it was reasonable to remove them from the analysis. The reason for the low juvenile recruitment at the river valley sites was not determined. Possible explanations for the low juvenile recruitment are: low birth rates or high rates of juvenile dispersal. Southern conspecifics have shown evidence of density-dependent birth rates (McCulloch and Inglis 1961), but whether this occurs in the Canadian kangaroo rat population is purely speculative. As well, juvenile banner-tailed kangaroo rats (*D. spectabilis*) have been shown to disperse less when population density is high (Jones et al. 1988). Therefore, dispersal may not explain the anomalously low number of juvenile recruits at the river valley sites. Alternatively, kangaroo rats at the river valley sites may have completed breeding activity earlier than other areas in the SNWA. Further research is necessary to determine whether low recruitment is caused by density-dependent population regulation, dispersal, or other mechanisms.

Effects on Survival

I expected bot fly parasitism to reduce survival of adult and juvenile kangaroo rats because kangaroo rats are an atypical host for *C. polita*. However, the results of my study

did not support my hypothesis; survival of parasitized kangaroo rats was not significantly different from nonparasitized kangaroo rats. Additionally, there were no significant interactions between parasitism and habitat type, sex, or body condition.

To conduct a comprehensive examination on the potential impact of bot fly infection on survival of kangaroo rats, I performed an individual-level (logistic regression analysis) and population-level (program MARK) survival analyses. In the individual-level analysis, I examined survival for two periods: overall and over-winter survival. I examined survival for two different periods because I could not assess survival in the period during the bot fly season until after the season ended (prior to winter). Kangaroo rats significantly reduced the amount of time spent above ground by September, so capture rates were too low in the fall to adequately examine summer survival. Consequently, whether mortality occurred during the bot fly season (perhaps directly from parasitism) or during the winter cannot be differentiated in the overall survival analysis. Regardless of the method of analysis, the results from both the individual-level and population-level analysis were consistent: bot fly parasitism was not significantly associated with survival of kangaroo rats.

Atypical hosts may experience higher mortality due to aberrant movement of the first instar larva (Dalmat 1943, Sillman 1959, Catts 1965, 1982), but I did not document higher mortality for parasitized kangaroo rats. However, if animals are killed due to aberrant movement of the first instar larva to its final location, then mortality would occur prior to knowing the animal was parasitized, and would thus be undetected. As a result, I cannot report if kangaroo rats are killed due to aberrant movement of first instar larvae.

The majority of field studies that examine the effects of bot fly parasitism on survival of natural hosts report that survival is not negatively affected. For example, survival of parasitized meadow voles was not significantly different from nonparasitized voles in studies by Clough (1965), Iverson and Turner (1968), and Getz (1970). In studies of the white-footed mouse, Wecker (1962), Goertz (1966), Clark and Kaufmann (1990), Munger and Karasov (1991), Jaffe et al. (2005), and Burns et al. (2005) report higher survival of parasitized mice. Conversely, Miller and Getz (1969) report reduced survival for parasitized mice. As well, studies on deer mice (Hunter et al. 1972, Jaffe et al. 2005), rock mice (Galindo-Leal 1997), and eastern chipmunk (*Tamias striatus*; Jaffe et al. 2005) also report higher survival of parasitized animals.

There are three theories as to why animals parasitized by bot fly larvae do not experience a reduction in survival: 1) parasitized animals reduce their movement and emigrate less, thereby decreasing predation risk and remaining on the study plot longer (Wecker 1962); 2) parasitized individuals alter their life history patterns, thus allocating resources to survival instead of reproduction (Burns et al. 2005); and 3) *Cuterebra* parasites and their respective hosts have co-evolved into a relationship that is not harmful to the host (Timm and Cook 1979).

Wecker (1962) suggested that survival of parasitized animals was not reduced because they were more sedentary than their nonparasitized counterparts. Since then, several authors have explored this hypothesis and found that movement of parasitized animals was not different than nonparasitized animals (Getz 1970, Hunter et al. 1972, Bennett 1973, Galindo-Leal 1997, Burns et al. 2005). I also examined this hypothesis, and found no significant difference between the maximum recapture distances of

parasitized and nonparasitized kangaroo rats. Therefore, the mobility of parasitized kangaroo rats was apparently not impaired.

Burns et al. (2005) hypothesize that bot fly parasitism induces a life history trade-off between current reproduction and survival. They found that parasitized white-footed mice had fewer and smaller litters, and suggest that survival was enhanced because mice diverted resources away from reproduction and put them towards body maintenance. I found evidence to suggest that juvenile recruitment of kangaroo rats was negatively affected by bot fly parasitism. Perhaps parasitized kangaroo rats diverted the energy that would have been expended for reproduction to facilitate survival. In any case, the extent to which kangaroo rats alter their life history in response to parasitism is purely speculative at this time and requires further investigation.

Parasites may alter normal activity patterns of their host, but such changes should not result in an increase in host mortality (Smith 1978d). In theory, a successful parasite will evolve a level of virulence that does not harm the host; after all, the survival of the parasite depends on the survival of the host (Jones 1967). However, I predicted that bot fly parasitism would significantly decrease kangaroo rat survival because the kangaroo rat is not the native host for *C. polita*. Laboratory studies demonstrate that bot fly parasitism can cause significant mortality in non-native hosts (see Smith 1977a, Baird 1979). Additionally, Boonstra et al. (1980) found that survival was significantly lower for parasitized Townsend's voles, and he suggested that this is because the bot fly parasite (which typically infects *Peromyscus* spp.) is not well adapted to the Townsend's vole. Perhaps significant mortality was not detected in kangaroo rats because *C. polita* is not specific to a particular species or group of closely related species as other *Cuterebra* spp.

In laboratory studies, Capelle (1970) demonstrated that *C. polita* was capable of successfully parasitizing animals other than the northern pocket gopher.

Another possible reason why I did not detect a significant reduction in survival of parasitized kangaroo rats may be because the winter during this study was particularly mild (personal observation). Kangaroo rats are typically not active above ground when temperatures are below -11°C and snow covers more than 40% of the ground, during which time kangaroo rats rely on their underground food stores (O'Farrell 1974). Because of the mild winter during this study, kangaroo rats would likely have continued to forage above ground throughout most of the winter. This almost certainly would have facilitated survival of nonparasitized and, possibly to a greater extent, parasitized kangaroo rats. I speculate that during a harsh winter, kangaroo rats that depleted their food cache to compensate for parasitism prior to winter could die of starvation because they would be unable to replenish it. Although Munger and Karasov (1994) determined that the energetic costs of bot fly parasitism were relatively small for the host, they suggest that if food was scarce or if the host experienced high energetic demands (e.g., cold stress) then negative effects would likely occur.

Conclusion

It is commonly asserted that bot fly parasitism may have detrimental effects on atypical hosts. However, the results of my study indicate that bot fly parasitism was not harmful for this atypical host at an individual level. Conversely, the results of my study revealed potential significant consequences at a population level because juvenile recruitment was negatively associated with bot fly parasitism. During this study, the bot fly season began when the majority of kangaroo rats completed breeding activity. As a

result, there may have been little impact on the population in this particular year.

However, in years when the bot fly and kangaroo rat breeding season coincide, the consequences for the population may be far-reaching. This is a very important consideration for the endangered northern kangaroo rat population and warrants further investigation.

CHAPTER 5

BOT FLY FIELD SURVEYS

INTRODUCTION

The behaviour of adult *Cuterebra* in the wild is known for only a few species, such as *C. latifrons* in California (Catts 1967), *C. polita* in Utah (Capelle 1970, Graham and Capelle 1970), *C. grisea* and *C. tenebrosa* in British Columbia (Hunter and Webster 1973), and *C. tenebrosa* in Washington (Baird 1974). Virtually nothing is known about the biology of adult *C. polita* in Alberta. To the best of my knowledge, adult *C. polita* flies have never been captured and have only been observed occasionally in Alberta (Gummer personal comm.).

In Utah, Capelle (1970) observed adult *C. polita* in the last week of July and the month of August. He reported that the flies were active for about three hours a day (starting ca. 9:30 am), once air temperatures reached 20°C, and the flies would disappear during periods of cloud cover. Graham and Capelle (1970) described the behaviour of male and female *C. polita* flies as follows: males typically positioned themselves on the terminal stems of shrubs in wait for female flies; and females searched for burrow openings in the vicinity of the males, and when a burrow was located, the fly would land at the opening and walk in.

My goal was to determine population size, seasonal and daily activity patterns, mating and flight behaviour, aggregation sites, and ovipositioning behaviour of adult *C. polita* at my study sites. However, I was unsuccessful in finding adult bot flies in the field. Alternatively, I also wanted to collect third instar larvae that emerged from kangaroo rats while they were handled, with the hope that I could rear and release them

and observe their behaviour. In this chapter, I present my field methods, results on reared larvae, and further recommendations for finding adult bot flies.

METHODS AND MATERIALS

Adult Bot Fly Surveys

I surveyed for adult bot flies and aggregation sites at a sub-set of my study sites in July 2004, and June and July 2005. Incidentally, kangaroo rats were showing signs of parasitism so I know that adult flies were active. I conducted my surveys on warm days with minimal cloud cover during the morning to mid-afternoon. In 2004, I selected one or two sites in each habitat type (sand dune, N2; river valley, N4; and road, A1 and A2) to survey for adult bot flies. In 2005, I surveyed at one sand dune and road site (N5 and A2, respectively; see Figure 1.2).

In 2004, I used three techniques to survey for adult bot flies: (1) foot searches along random transects, (2) non-random foot searches, and (3) pitfall traps. The behaviour and habitat use of adult bot flies in Alberta is unknown, so I first conducted foot searches along random transects within kangaroo rat habitat and the surrounding area. Random transects involved slowly walking 500-1000 m with an insect net to capture all insects resembling a bot fly. Along each transect, I recorded the date, time, distance, temperature, wind speed, cloud cover, vegetation description, and presence of kangaroo rat burrows and gopher mounds. I also conducted non-random searches to examine specific areas for adult *C. polita*. These were areas with a high density of shrubs and kangaroo rat burrows. Using an insect net, I captured and identified all large insects resembling a bot fly.

I also designed and set pitfall traps to increase the chance of capturing adult female bot flies. I constructed pitfall traps out of tin cans and PVC tubing. A screen funnel was inserted in one end; the other end was kept closed to prevent escape. I set 10 traps in kangaroo rat burrows, and made 10 'artificial' burrows by digging a hole and placing the trap inside. I set the traps in the morning (ca. 08:00-10:00), checked them regularly, and dismantled them in the early afternoon (ca. 13:00-14:00). I did not attempt to use malaise traps baited with CO₂ because this technique has proven to be unsuccessful in attracting adult *C. polita* (Capelle 1970, Graham and Capelle 1970). In 2005, I focused all my efforts on non-random searches to locate adult bot flies because the random foot searches and pitfall capture methods were unsuccessful.

Bot Fly Egg Searches

In 2005, I also examined kangaroo rat burrows for the presence of bot fly eggs. *Cuterebra* eggs are approximately 1 mm long and 0.3 mm wide, dull white, and flattened (Capelle 1970). Despite the small size of the eggs, other researchers have observed them in the environment (Catts 1967, Capelle 1970, Graham and Capelle 1970, Baird 1974). Excavation of two pocket gopher burrows by Capelle (1970), revealed that the eggs were deposited on plant roots 30-50 cm from the burrow opening. One of the excavated burrows contained 29 eggs, the other only two (Capelle 1970).

I selected one sand dune site (N5) and road site (A1) to look for the presence of bot fly eggs in kangaroo rat burrows. I visually inspected burrows and runways for the presence of bot fly eggs. I used an angled mirror and a flashlight to look inside the burrows. I paid special attention to the roots hanging from the ceiling of the burrow. On the final day of examination, I scraped a 30 cm length of the ceiling of each burrow with

a bristled brush in a modified tube with a plastic bag attached to the end to catch the falling debris. I then poured the contents of each bag into a separate tray and sifted through the debris looking for the presence of bot fly eggs.

Reared Larvae

Mature third instar bot fly larvae will sometimes emerge while handling parasitized kangaroo rats. As a result, larvae can be collected for rearing into adult flies. During the 2004 bot fly season, I collected 13 third instar bot fly larvae that emerged while handling kangaroo rats. I put each larva in a glass jar or plastic container filled with sand. When placed on the surface of the sand, the larvae would immediately bury themselves. There are limited reports on the conditions required to rear bot fly larvae. However, Smith (1977a) successfully reared bot fly larvae kept refrigerated at about 6°C. I kept containers and jars containing six larvae in a walk-in cooler (at a constant temperature of 4 ± 1 °C) at the University of Calgary. I buried the remaining containers of larvae at a sand dune to provide the pupating larvae with natural environmental conditions. The containers were buried just below the surface of the sand. In the early spring, I put a screen cage over the area to capture any emerging flies.

RESULTS AND DISCUSSION

Adult Bot Fly Searches

In 2004, I completed non-random searches and random transects on five days (approximately 2.5 hrs/day), which included approximately 5 km of non-random searches and 32 (17 km) random transects. I set pitfall traps on four days, 20 traps/day. I did not find adult bot flies with any method. In 2005, I completed five days of non-random

searches. Again, no adult bot flies were found. Despite the obviousness of the larvae, the adults are frequently described as difficult insects to find in nature (Cameron 1926, Dalmat 1943, Sillman 1955, Catts 1967, Baird 1974, Catts 1982, Colwell et al. 2006).

My lack of success in finding adult bot flies was possibly due to insufficient survey effort. However, inclement weather prevented me from conducting daytime surveys at the end of June and early July. As well, it was too difficult to conduct both night-time surveys for kangaroo rats and daytime surveys for adult bot flies. Additionally, there may only be a small number of flies active on any given day. Field surveys for adult bot flies often report low densities. For example, Catts (1967) observed only 3 to 15 males per day; Capelle (1970) observed 15 – 45 adults per day; Graham and Capelle (1970) captured an entire population on two occasions, yielding 20 and 32 individuals respectively; and Baird (1974) only saw 5 to 7 males active at a site on a single day, and only the occasional female. Therefore, I may not have found adult bot flies because I could not allocate enough time to search during the day, and their relatively small numbers would have contributed to my poor results.

Alternatively, I may not have surveyed at the correct time of year or day. My searches for adult bot flies occurred when the bot fly parasitism season already began (i.e., July 12, 2004), which may have been too late in the season. However, the timing of adult activity and the infection period can coincide (Graham and Capelle 1970, Baird 1974). For example, Graham and Capelle (1970) captured parasitized gophers and adult *C. polita* concurrently between late July and August. Furthermore, I may not have surveyed at the correct time of day. However, I conducted my surveys in the morning to mid-afternoon, when temperatures were above 20°C, the timing reported by Capelle

(1970) and Graham and Capelle (1970) in Utah. It is possible that *C. polita* in Alberta has different daily activity patterns than in Utah because bot flies have been observed to be active in the late afternoon and early evening (Baird 1974).

Bot Fly Egg Searches

I began the visual inspection of burrows for the presence of bot fly eggs on July 15, 2005. I examined burrows every 3–4 days for the following two weeks. Incidentally, the first observations of infection in kangaroo rats occurred during night-time surveys in the same period; therefore, I knew that *Cuterebra* eggs must have been present in my study area. However, I was unable to detect bot fly eggs in the burrows of kangaroo rats. The visibility within burrows varied and depended on the diameter of the burrow and whether the tunnel was straight or curved. Overall, I could only see about 20–40 cm inside the burrow. As well, I did not detect bot fly eggs in the debris collected from scraping the ceiling of each burrow. I also did a visual inspection of the vegetation surrounding the burrows and along kangaroo rat runways for the presence of bot fly eggs. None were detected. Catts (1967) was able to see *Cuterebra* eggs within 30 cm of the opening of wood rat tunnels. I speculate that the eggs of *C. polita* are deposited too deep within the burrow to visually detect.

Reared Larvae

Only 3 of the 13 larvae (all from the cooler) successfully emerged as an adult: 1 female larva collected on August 16, and 2 male larvae collected on July 29 and August 20, 2004. All of the adults emerged during the week of July 11, 2005. Based on these results, the pupation time ranged from 325–347 days, supporting the findings of Capelle (1970) and Gummer et al. (1997).

I unsuccessfully attempted to induce mating between the female and each male separately, using the tumbled confinement method described by Smith (1973). The female lived for five days and one male lived for only two days, the other three days. These specimens were pinned and submitted to the Royal Museum of Alberta. Because only three adults emerged, and they did not survive very long, I did not release them in the field to observe their behaviour.

RECOMMENDATIONS FOR FUTURE RESEARCH

Evidently, more daytime searches are necessary to find adult *C. polita* in the field. It is possible that adult bot flies in Alberta follow different seasonal and daily activity patterns than those reported for *C. polita* in Utah. I recommend that surveys for adult bot flies begin in the early spring, perhaps every four or five days. This should continue throughout the parasitism season in order to determine the adult flies' active season. As well, searches throughout the daytime are needed to determine daily activity patterns. Studies of adult bot flies report that the active time is mid-morning to early afternoon (*C. latifrons*; Catts 1967, *C. polita*; Capelle 1970). In contrast, Baird (1974) reported that *C. tenebrosa* was active in the late afternoon and early evening.

I recommend the use of pitfall traps in burrows to attempt to capture mated females, even though I failed with this method. If female bot flies deposit their eggs in burrows, then this method should be effective.

When adult flies are found in the field, mark-recapture surveys could be conducted to determine population characteristics, such as sex ratio, population size, and behaviour. Catts (1967) and Baird (1974) both marked bot flies on the notum with white

ink and released them in the field. They were able to successfully conduct a mark-resight survey and study the flies' activity patterns.

CHAPTER 6

SUMMARY, SYNTHESIS, RECOMMENDATIONS FOR FUTURE RESEARCH, AND MANAGEMENT IMPLICATIONS

SUMMARY OF RESEARCH

The natural habitat of the Canadian population of Ord's kangaroo rat is becoming increasingly rare, evidently due to changes in climate, fire, and ungulate grazing. In addition, kangaroo rat habitat has also been highly disturbed by the development and maintenance of roads. Roads provide the open, sandy habitats that kangaroo rats require, and consequently kangaroo rats have become relatively abundant along roads.

Observations from kangaroo rat surveys suggest that there may be a disadvantage to living along roads. Specifically, kangaroo rats captured in road habitat appeared to be more heavily parasitized by bot fly larvae than kangaroo rats living in natural areas. These observations were of particular importance because bot flies are typically specific to a particular host species or a group of closely related species, but kangaroo rats are not considered to be associated with bot fly parasites (Catts 1982).

Interestingly, the Canadian kangaroo rat population is the only one observed to be parasitized by bot fly larvae. Therefore, kangaroo rats may not be a suitable host for this parasite and may experience detrimental effects. The objectives of my thesis were to: (1) document the temporal pattern of parasitism, prevalence and intensity, and the site of warble development in kangaroo rats; (2) determine if bot fly parasitism in kangaroo rats was related to habitat type and connectivity of habitat; (3) determine the effects of bot fly parasitism on body condition, reproduction, and survival of kangaroo rats; and (4)

observe and document activity patterns and behavioural characteristics of the adult bot fly.

From a sample of 707 individual kangaroo rats surveyed in 2004, kangaroo rats were parasitized by bot fly larvae between July 12 and October 13. Bot fly prevalence in kangaroo rats was estimated at 30% during this period. Prevalence did not differ significantly between the sexes and age groups of kangaroo rats. The average intensity was 1.8 and the maximum intensity was 7. The majority of kangaroo rats carried only one bot and intensity did not differ between sex and age groups. Bot fly larvae were most commonly located in the hips, abdomen, and along the sides of the kangaroo rat's body.

In this study bot fly prevalence and intensity were not significantly associated with habitat connectivity. However, bot fly prevalence differed significantly among the different habitat types (i.e., roads, sand dunes, and river valleys). Mean prevalence was similar between sand dune and road habitats but was significantly lower at river valley habitat. However, prevalence varied considerably among the sand dune sites and was more consistent among the road sites.

I predicted that parasitism by bot fly larvae would have detrimental effects on the life history traits of kangaroo rats because of the atypical host-parasite relationship. Contrary to my prediction, bot fly parasitism was not significantly associated with the body condition, reproductive status, and survival of individual kangaroo rats. However, bot fly parasitism was negatively correlated with the estimated measure of juvenile recruitment. I found that sites with higher prevalence had a lower juvenile/adult female ratio than sites with lower prevalence.

I attempted to find adult bot flies and bot flies eggs at my study sites.

Unfortunately, I was unable to find bot fly adults or eggs in the field. I also made an attempt to rear bot fly larvae from larva that was collected while processing kangaroo rats. I collected 13 bot fly larvae, but only three were successfully reared as adults, one female and two males. The pupation time for these individuals was 325-347 days.

SYNTHESIS

Kangaroo rats experienced parasitism regardless of habitat type, although prevalence at the river valley habitat type was significantly lower. I speculate that the heterogeneity in prevalence among habitat types was due to the amount of vegetation cover present. *Cuterebra polita* females rely on visual cues to locate the burrows of potential hosts to deposit eggs and the visibility of burrows most likely influences the encounter rate. Prevalence was high in habitats (i.e., sand dunes and roads) with open bare sand and little vegetation cover and the burrows were generally very conspicuous. In comparison, prevalence was significantly lower in habitats (i.e., river valley areas) that were more heavily vegetated and the burrows were generally more hidden. Differences in prevalence among habitats did not appear to be associated with host density, the movement of transient individuals, or microclimate factors. Undoubtedly, there may be other reasons for the observed differences in prevalence among habitat types that were not explored in this study.

Kangaroo rats did not demonstrate the pathology typically described for atypical hosts, specifically the warble structure and site development, and significant loss of body mass and mortality. For example, in atypical hosts the structure of the warble is described

as being soft and gelatinous (Catts 1982). The warble in kangaroo rats was similar to those described for natural hosts: well defined in a thickly-walled cyst that is clean, dry, and surrounded by a small area of denuded skin (Catts 1982). Additionally, in atypical hosts the site of warble development tends to be inconsistent (Catts 1982). For example, during a host-specificity study the larvae developed on the neck, face, and back of the atypical host (dusky-footed woodrats), and in the native host (bushy-tailed woodrat) larvae were located on the back and sides (Baird 1979). In kangaroo rats, the larvae were most commonly located in the hips, abdomen, and along the sides of the body, which was similar to the site of warble development in pocket gophers (Richens 1965, Graham and Capelle 1970). Furthermore, atypical hosts allegedly experience significant weight loss and higher mortality (Catts 1982). Conversely, in this study I did not detect a significant loss of body mass and parasitism was not significantly associated with kangaroo rat survival. However, the absence of negative effects on survival may have been confounded by the particularly mild winter. Therefore, it is important to consider that bot fly parasitism may have detrimental effects on survival during years when there are harsh winter conditions.

I did not detect detrimental effects of bot fly parasitism on kangaroo rats at the individual-level, but perhaps more importantly, the association may impact kangaroo rats at a population-level. I found evidence to suggest that bot fly parasitism may reduce juvenile recruitment because prevalence was negatively correlated with the number of juveniles per adult female, even though parasitized females displayed external signs of reproductive activity. As well, anecdotal observations that a small number of kangaroo rats that were pregnant or lactating when they became parasitized did not successfully

rear their young corroborate these results (see Chapter 4). Therefore, parasitism may be a significant threat to the persistence of the kangaroo rat population. Incidentally, during this study the bot fly season and the breeding season did not entirely coincide. However, in years when there is more overlap, I hypothesize that a parasite-induced reduction in juvenile recruitment and consequently the impacts on population growth would be evident.

One of the limitations of this study was that it examined the relationship between kangaroo rats and *C. polita* over a very short time period. Variability in the timing of parasitism, prevalence, intensity, and effects certainly exist in this association. However, the results of this study likely fall within the range of natural variability. This study occurred when food resources were presumably high, the period of parasitism and kangaroo rat breeding season did not coincide greatly, and the winter was mild. Consequently, this may be why I did not detect significant negative effects on body condition, reproduction, and survival.

The availability of resources for kangaroo rats and climate most likely influence this association to a large extent. For example, a harsh winter may exacerbate the impacts of bot fly parasitism on kangaroo rats because of the energetic stress and starvation. Additionally, if the breeding season and parasitism season overlap, the energetic costs and physical hindrance of bot fly parasitism may reduce the reproductive potential of parasitized kangaroo rats. Finally, a lack of resources during the parasitism season would likely negatively affect the body condition and food cache of parasitized kangaroo rats, thus leading to higher mortality. Therefore, it is important that long-term studies are

carried out on this parasitic relationship because this study does not correspond to all circumstances and extreme weather or shifting seasons may influence the results.

RECOMMENDATIONS FOR FUTURE RESEARCH

This was the first study on the potential effects of bot fly parasitism in Ord's kangaroo rat. Since this population is endangered, any potential factors that may be affecting population dynamics should be thoroughly examined. There are several topics that I think warrant further research to increase our understanding of this host-parasite relationship and determine the severity of parasitism on the kangaroo rat population:

- 1) It is imperative to examine the effect of bot fly parasitism on the reproductive success of kangaroo rats. A more direct measure of reproductive success should be used. Specifically, litter number, litter size, and number of recruits should be determined for a group of parasitized and nonparasitized mothers, and comparisons made.
- 2) Long-term studies are necessary to examine the effects of bot fly parasitism on population growth of kangaroo rats. As well, comparisons could be made between populations at different habitat types.
- 3) Longer term studies are also necessary to determine the potential influence of climate change and variability of resources (i.e., will the impacts of parasitism become apparent in years with harsh winters or low resource availability) on prevalence and the effect of parasitism on survival, body mass, and reproduction.
- 4) Further investigation into the degree of bot fly infection in northern pocket gophers and other small mammals is necessary to identify the host specificity of *C. polita*.

- 5) Further investigation is needed to examine if the habitat differences in prevalence are related to the conspicuousness of kangaroo rat burrows or if there are other, yet to be identified, contributing factors in the selection of burrows.
- 6) The biology of the adult bot fly should be studied to increase our understanding of this parasite.

MANAGEMENT IMPLICATIONS

In order to determine if bot fly parasitism is impacting population growth and persistence, long-term annual monitoring is needed. Annual monitoring of specific kangaroo rat populations at different habitat types will provide the data necessary to determine population trends, and determine if population declines are correlated with bot fly prevalence. It is imperative that such monitoring is completed from spring through to fall in order to ensure animals are monitored during the bot fly season. Long-term monitoring will assist in determining the impact of bot fly parasitism in years when the bot fly and breeding season coincide, winters are harsh, and there is low resource availability.

The areas along the South Saskatchewan River valley appear to be an important habitat for kangaroo rats. Bot fly prevalence was extremely low in these areas and kangaroo rat density was very high. Therefore, these areas should receive high priority for conservation and protection against industrial activities.

Results from this study showed that bot fly parasitism rates were consistently high at road sites. Roads likely represent prime habitat for the bot fly, and it is possible that sandy roads are facilitating the spread of this parasite. Therefore, the impacts on the

kangaroo rat population should be considered if new access routes (i.e., sandy roads) are planned in the kangaroo rat's range.

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