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DETERMINANTS OF AGE AT DISPERSAL AND
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SQUIRREL, SPERMOPHILUS BELDINGI

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DETERMINANTS OF AGE AT DISPERSAL AND SETTLMENT PATTERNS IN THE BELDING'S GROUND SQUIRREL, *SPERMOPHILUS BELDINGI*

By

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ABSTRACT

DETERMINANTS OF AGE AT DISPERSAL AND SETTLMENT PATTERNS IN THE BELDING'S GROUND SQUIRREL, *SPERMOPHILUS BELDINGI*

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Mammalian dispersal often occurs before individuals reach sexual maturity, when they are smaller and less experienced than post-pubertal animals, and thus more vulnerable to dispersal risks. Predominant early dispersal among mammals suggests that dispersers gain a selective advantage by emigrating at a young age rather than delaying emigration until they are older. For example, early dispersal may allow emigrants to reduce the social resistance they encounter from local residents during the immigration process. The Belding's ground squirrel, *Spermophilus beldingi*, exhibits a dichotomous dispersal pattern: most males disperse at 7 - 10 weeks of age, as juveniles, but some males delay emigration until they are 55 weeks old, as yearlings. I was therefore able to use this species to assess whether young immigrants experience less social resistance from resident adults than do older immigrants. During staged encounters, female residents directed lower rates and intensities of aggression towards juvenile than yearling males. During natural encounters, resident females were less likely to aggress against juvenile than yearling males during an encounter. These results suggest that early dispersal is adaptive for male *S. beldingi* by allowing juvenile immigrants to avoid aggression from female residents more effectively than can males who disperse as yearlings.

Predominant early dispersal among mammals also suggests its risks may be offset by significant fitness gains. I used long-term trapping data and behavioral observations of *S. beldingi* males during the breeding season to assess the consequences of dispersal age on male survival and mating success. I found that age-specific survivorship was only lower among early than late dispersers to age one, but early dispersers mated with a greater number of different females than did late dispersers. These data illustrate that early dispersal carries a small cost to short-term survival, but ultimately enhances mating success for surviving males.

Because natal dispersal may be dangerous, natural selection should shape this behavior to occur in each species at an age when emigrants are best able to cope with its risks and challenges. I examined the role of life history, social, and ecological factors in shaping the evolution of dispersal age in ground-dwelling sciurid rodents. Data from 22 species were extracted from the literature, and analyzed after computing phylogenetic independent contrasts to control for non-independence of data points due to common ancestry. I found that the amount of growth males were able to complete during their juvenile summer had a significant negative effect on the age at which males dispersed. I also observed a positive relationship between the level of social resistance immigrants were likely to encounter and a species' dispersal age. However, I found no significant relationship between mean dispersal distance, a measure of dispersal risk, and the age at which a particular species generally disperses.

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CHAPTER ONE

GENERAL INTRODUCTION

Natal dispersal, the permanent departure of an individual from its birthplace, occurs in most birds and mammals (Greenwood, 1980; Lidicker, 1975). This behavior represents a key event in the life history of an individual and has critical effects on the persistence of populations and species (Colbert et al., 2001; Greenwood, 1980). For an individual, dispersal minimizes inbreeding and increases reproductive opportunities (Dobson, 1982; Lehmann and Perrin, 2003; Moore and Ali, 1984; Pusey, 1987; Shields, 1982). The influx of dispersers also enhances the viability of a population and reduces the chance of local extinction (Hanski, 1999). Even if local extinction occurs, dispersers are frequently able to re-colonize previously occupied areas (Roach et al., 2001).

Natal dispersal tends to be sex-biased in that one sex is usually more likely to disperse or disperses over greater distances than the opposite sex (Dobson, 1982; Greenwood, 1980). In birds, females, and in mammals males, tend to be the predominant dispersing sex. Furthermore, the age at which dispersal occurs tends to be highly predictable within a species. Despite the importance of dispersal, our knowledge of this behavior is still limited, and very little is known about the factors that determine the age at which dispersal occurs among most animal species. The objective of my dissertation is to fill this gap by examining what variables determine age at dispersal in the Belding's ground squirrel, *Spermophilus beldingi*, and other ground dwelling sciurids.

Dispersal is a critical event in the life of an animal since it represents one of the most profound environmental changes an individual is likely to experience during its lifetime. A disperser leaves the safety of a familiar social and physical environment and must navigate through unfamiliar habitat where it is exposed to many mortality factors such as predation and lack of essential resources. After the individual has located a suitable settlement site, the emigrant must rapidly gather and assimilate knowledge of the social and physical features of its new home to ensure successful settlement (Isbell and Van Vuren, 1996; Van Vuren and Armitage, 1994; Waser and Jones, 1983a). The costs of dispersal can be substantial and may include exclusion from important resources (Garrett and Franklin, 1988), loss of reproductive opportunities (Alberts and Altmann, 1995), injury, and even death (Byrom and Krebs, 1999). Considering its potential costs, an individual's decision on when to embark on this journey should have significant consequences for a disperser. Although our knowledge of dispersal behavior is still limited, a number of studies have succeeded in identified factors that mediate dispersal behavior (e.g., Holekamp, 1986); see also review in Dufty and Belthoff, 2001). These studies have also provided insights into the variables that might determine age of dispersal in birds and mammals.

The role of body condition in mediating natal dispersal has been documented in a number of avian and mammalian species. In the marsh tit, individuals with better body composition disperse at younger ages than do individuals in poorer condition (Nilsson and Smith, 1985). Larger individuals are more likely to emigrate than smaller individuals in the greater flamingo (Barbraud et al., 2003). Dominance is tightly coupled with body condition in screech owls, and dominant individuals disperse at younger ages than subordinates (Ellsworth and Belthoff, 1999). An association between body mass, body condition, and dispersal behavior has also been observed in a number of mammalian studies (see review by Holekamp, 1984a). For example, in the hibernating Belding's ground squirrel body mass and body fat regulates dispersal behavior of males. Males that are able to reach a specific body mass/body fat threshold early during their first active season disperse prior to their first hibernation (Nunes et al., 1998; Nunes and Holekamp, 1996). However, males that are unable to reach this fat threshold until later in the season postpone dispersal until after their first hibernation. Overall, these studies suggest that body condition determines dispersal age such that individuals with adequate energy resources disperse at younger ages than do individuals in poor condition.

Considerable evidence suggests that endocrine secretions regulate dispersal behavior by organizing and activating the neural circuits responsible for the expression of this behavior. Organizational effects of gonadal steroids on sexual differentiation of male or female behavior have been demonstrated in birds and mammals (e.g., Adkins-Regan, 1987; Phoenix et al., 1959). Since dispersal tends to be sexual dimorphic, gonadal steroids might therefore be expected to play a similar role in organizing dispersal behavior in these taxa (Holekamp and Sherman, 1989). This has shown to be the case in the grey-sided vole, *Clethrionomys rufocanus*, where females exposed to high levels of testosterone in utero are more likely to disperse than females with low exposure to testosterone (Ims, 1989). In Belding's ground squirrels, females treated experimentally with testosterone exhibit the male-typical dispersal pattern, supporting the hypothesis that testosterone organizes dispersal behavior in this species (Holekamp et al., 1984; Nunes et al., 1999).

The correlation between sexual maturation, increases in circulating testosterone, and the onset of dispersal suggest that testosterone may be involved in activating this behavior in some mammalian species (reviewed in Dufty and Belthoff 2001; but see (Holekamp and Smale, 1998). In many avian species, however, dispersal occurs once gonads have regressed, and male mammals often disperse before reaching puberty (Dobson, 1982). Consequently, it is unlikely that gonadal steroid hormones have an activational affect on dispersal behavior in a large number of avian and mammalian species. Instead, hormones that function as primary signals in energy balance may trigger this behavior. For example, the hormone leptin is produced by fat cells, and high leptin titers in the blood indicate large fat stores (Caro et al., 1996). Leptin may therefore trigger dispersal behavior in species, such as the Belding's ground squirrel, where a fat threshold determines the onset of dispersal behavior (Nunes and Holekamp, 1996). However, circannual timing mechanisms appear to override the activational signal in the Belding's ground squirrel since males that reach this fat threshold late in the season delay dispersal until after their first hibernation (Nunes et al., 1998). Hence, the neural circuitry responsible for regulating dispersal behavior is most likely similar across dispersers of different age groups. Yet, the sensitivity of individuals to the activational signal may vary based on seasonal or environmental factors.

External environmental factors may also mediate dispersal behavior. For example, aggression directed towards dispersers at their natal site may trigger emigration. This appears to be the case in species where the immigration of an adult male leads to the eviction of young residents (red howler monkeys, *Alouatta seniculus,* Crockett and Sekulic, 1984; guanacos, *Lama guanicoe,* Sarno et al., 2003). Avoidance of potential competitors such as littermates or lack of social bonds with close relatives may also mediate dispersal behavior. However, only few studies have provided support for these hypotheses (e.g., Barash, 1989) suggesting that these factors may play a limited role in regulating dispersal behavior (Holekamp, 1984). In the Belding's ground squirrel, neither aggression from conspecifics at the natal site nor avoidance of competition with relatives mediate dispersal behavior of males (Holekamp, 1986). However, resident aggression towards immigrants may influence dispersal success of individuals. Social resistance towards potential emigrants has been documented in a large number of species (e.g., lions, *Panthera leo*, Hanby and Bygott, 1987; golden lion tamarins, *Leontopithecus rosalia*, Baker and Dietz, 1996; common mole rats, *Cryptomys hottentotus hottentotus*, Spinks et al., 2000; coyotes, *Canis latrans*, Gese, 2001) and the age of the immigrant appears to influence an individual's ability to counter or elude this aggression. In the meerkat, *Suricata suricatta*, and the dwarf mongoose, *Helogale parvula*, males that disperse when they are very young are less likely to encounter aggression than males that immigrate into a pack as fully grown adults (Doolan and Macdonald, 1996; Rood, 1987). In mammals, natal dispersal typically occurs before individuals reach sexual maturity (Dobson, 1982). Hence, early dispersal in mammals may occur because this permits young males to better avoid social resistance during the immigration process.

Considering its potential costs, it is reasonable to assume that natural selection should have shaped dispersal behavior to occur at an age that maximizes an individual's fitness. Furthermore, selection should have acted on this dispersal behavior to occur in species at an age when emigrants are best able to cope with its risks and challenges. Alternatively, however, natural selection may have had little influence on determining the age at which this behavior occurs among individuals and species. This may be the case if dispersers are forced from their natal site or if a developmental error alters the neural circuitry that regulates this behavior. As a result, dispersal may occur before individuals have reached an age when their dispersal prospects are optimal. If this is the case, dispersal age should not influence a disperser's fitness and dispersal ages across related species should exhibit a random pattern. It is possible to asses the role of natural selection in shaping this behavior by examining the fitness consequences of age at dispersal and by assessing the role of selective agents in shaping dispersal age across a broad range of species.

OVERVIEW OF CHAPTERS

The Belding's ground squirrel exhibits the sexually dimorphic dispersal pattern typical of most mammals but also shows an age-specific bimodal dispersal pattern; 70 – 90% of males disperse as juveniles at 7-10 weeks of age while 10 – 30 % of males emigrate the following summer as yearlings around 55 weeks of age. All males leave home before they reach reproductive maturity at 2 years of age (Holekamp, 1986). Much is known about this species' life history, social, reproductive, and dispersal behavior. Consequently, *S. beldingi* provides an ideal model system to examine the factors that might determine dispersal age in mammals.

In chapter two, I used the Belding's ground squirrel to assess whether young immigrants experience less social resistance from resident adults than do older immigrants while searching for and settling in new homes. I used staged and naturally occurring encounters to examine responses by residents towards juvenile and yearling dispersers. During staged intruder experiments, lactating females were more aggressive towards yearling than juvenile males. This difference disappeared when the breeding season ended. Intruders in both age groups encountered adult resident males at higher rates than resident females, but resident females were more aggressive to them than were male residents, particularly towards yearling intruders. Adult male residents were equally likely to aggress against juvenile and yearling male intruders. These results indicate that early dispersal is adaptive for male *S. beldingi* by allowing juvenile immigrants to avoid aggression from female residents more effectively than can males who disperse as yearlings.

Predominant juvenile dispersal among mammals suggests its risks may be offset by significant fitness gains. In chapter three, I inquired whether dispersal at a young age enhances male fitness in the Belding's ground squirrel. The dichotomous dispersal pattern of this species provides an opportunity to assess the influence of dispersal age on male fitness by comparing survival and reproduction between early- and late-dispersing males. I used live-trapping data collected between 1993 and 2003 to inquire whether dispersal at a young age enhances male survival. In 1998, extensive mating observations were conducted to assess differences in male mating success based on male dispersal age. I found that age-specific survivorship varied significantly among early and late dispersers, which was primarily due to significant lower juvenile survivorship for early- than late-dispersing males. The probability of observing a male mating in 1998 did not differ between early and late dispersers, but early dispersers mated with a greater number of different females than did late dispersers. Overall, these data indicate that early dispersal may carry significant survival costs early in life, but ultimately enhances mating success for surviving males.

Because natal dispersal may be dangerous, natural selection should shape this behavior to occur in each species at an age when emigrants are best able to cope with its risks and challenges. In Chapter four, I examined the role of life history, ecological, and social factors in shaping the evolution of dispersal age in ground-dwelling sciurid rodents. Specifically, I tested three hypotheses that have been invoked to explain variation in dispersal age among species of this group. The growth limitation hypothesis posits that dispersal age of ground-dwelling sciurids is determined by growth constraints imposed by life history and environmental factors. Aggression by local residents can influence immigration success, and the social resistance hypothesis suggests this aggression may have acted as an important selective agent shaping dispersal age in sciurids. Lastly, mortality during transit and early settlement can be high for dispersers, and the risk avoidance hypothesis suggests that risks associated with increasing dispersal distance may affect the age at which individuals emigrate. I reviewed the literature on ground-dwelling sciurids for field studies that documented dispersal age and reported other relevant information. I then used the extracted data from 22 species to test the predictions of the dispersal constraint hypotheses. Data were analyzed after computing phylogenetic independent contrasts to control for non-independence of data points due to common ancestry. In support of the growth limitation hypothesis, I found that the amount of growth relative to adult body mass males were able to complete during their juvenile summer had a significant negative effect on the age at which males dispersed. I also observed a positive relationship between the level of social resistance immigrants were likely to encounter and a species' dispersal age, a result supporting the social resistance hypothesis. However, I found no significant relationship between mean dispersal distance, a measure of dispersal risk, and the age at which a particular species' generally disperses. Overall, these results shed light on the selective forces that have shaped the evolution of dispersal behavior in mammals.

CHAPTER TWO

EARLY DISPERSAL REDUCES RESIDENT AGGRESSION DIRECTED TOWARDS IMMIGRANT MALE BELDING'S GROUND SQUIRRELS (*SPERMOPHILUS BELDINGI*)

INTRODUCTION

Natal dispersal, the permanent departure of an individual from its birthplace, occurs in most birds and mammals (Greenwood, 1980; Lidicker, 1975). Emigration from the natal area reduces the probability of inbreeding and increases the probability of encountering potential mates (Lehmann and Perrin, 2003; Moore and Ali, 1984; Pusey, 1987; Shields, 1982). Dispersal is often risky for individuals as they leave behind the safety of a familiar social and physical environment, travel through potentially inhospitable terrain, and settle in unfamiliar places where resources needed for survival and reproduction must be found anew (Isbell and Van Vuren, 1996; Van Vuren and Armitage, 1994; Waser and Jones, 1983a). Dispersers may also encounter xenophobic or hostile conspecifics inhabiting areas in which emigrants might choose to settle (e.g., Garrett and Franklin, 1988). In mammals, natal dispersal tends to be male biased, with males dispersing at higher rates and over longer distances than females (Greenwood, 1980; Lidicker, 1975). Surprisingly, male mammals often disperse before they reach sexual maturity (Dobson, 1982). Thus dispersers must often cope with the challenges of dispersal even before they have completed their own growth and maturation.

Aggression directed by local residents at prospective immigrants can prevent dispersers from successfully settling in a new area or group (e.g., lions, *Panthera leo*, Hanby and Bygott, 1987; golden lion tamarins, *Leontopithecus rosalia*, Baker and Dietz, 1996; common mole rats, *Cryptomys hottentotus hottentotus*, Spinks et al., 2000; coyotes, *Canis latrans*, Gese, 2001). Such aggression can result in injury or death, and may also force dispersers to use energy reserves that may already be severely limited (Drews, 1996; Holekamp, 1986; McNutt, 1996; Packer, 1979). Behavioral strategies adopted by some dispersers reduce aggression directed at them by local residents. For example, some male primates select new troops to join based on their own personal histories of friendly interactions with members of those groups during previous encounters (e.g., Cheney, 1983). When traversing strange habitat, dispersers may also modify their behavior in a manner that reduces resident aggression. Immigrant male spotted hyenas (*Crocruta crocruta*), for example, sometimes face intense aggression from residents, and they consistently exhibit extreme unsolicited appeasement behavior upon entry into the territory of a strange clan (Smale et al., 1997). In some species, natal dispersal tends to occur during periods each year when intraspecific aggression is infrequent, such as during the non-breeding season (e.g., some marsupials, Cockburn et al., 1985). Thus selection may often favor life history traits that minimize the probability that immigrants will encounter social resistance from resident animals.

Here, I studied Belding's ground squirrels, *Spermophilus beldingi*, to inquire whether resident aggression might have acted as a selective agent affecting age at dispersal in gregarious mammals. *S. beldingi* offer an excellent model system in which to examine variation in resident aggression encountered by dispersing males. This species not only exhibits the sexually dimorphic dispersal pattern characteristic of most mammals, but also an age-specific bimodal dispersal pattern; 70–90% of males disperse as juveniles at 7-10 weeks of age whereas 10–30% of males emigrate the following year as yearlings, at around 51-55 weeks of age (Holekamp, 1984b). All males leave home before they reach adult male body size, at the end of their second active season, and before they start mating at 2 years of age, and before they achieve adult body mass (Holekamp, 1986; Sherman, 1976). Juvenile males disperse at the end of their first summer, when agonistic interactions among adults typically occur at low rates. By contrast, yearling males disperse early in the season, shortly after emerging from their first hibernation, during the breeding season. Thus, yearling dispersers may attempt to settle in new areas when adult males exhibit high rates of aggressive behavior while competing for mates, or immediately after mating when aggression peaks among females as they begin to set-up and defend territories (Nunes et al., 2000; Sherman, 1976; Wolff and Peterson, 1998).

My objective was to test the hypothesis that the age at which dispersal occurs influences the social resistance encountered by male immigrants. I compared resident responses towards juvenile and yearling male *S. beldingi* during staged experimental encounters between tethered "intruders" and resident adult females, and also during naturally-occurring encounters between residents and intruding males in each age class. Since most male *S. beldingi* disperse as juveniles, my hypothesis predicted in staged encounters that adult females would be more likely to aggress against, and direct higher rates or intensities of aggression towards, yearling than juvenile males. My hypothesis also predicted that residents would be more likely to aggress against yearling than juvenile intruders during naturally-occurring encounters. Because males of the two dispersal groups leave home at different ages, and during different portions of the species' active season, I performed three additional comparisons to tease apart the influence of age and season on responses by residents towards male intruders. In staged encounters, I compared responses of adult females towards intruders between breeding and post-breeding seasons. In addition, I compared resident responses towards yearlings during naturally-occurring encounters that took place during the breeding and post-breeding seasons. Lastly, during naturally-occurring encounters, I compared resident responses towards yearling males grouped on the basis of the age at which they had dispersed. That is, I compared responses by residents towards yearling males that had dispersed early (as juveniles) to their responses towards yearling males that had dispersed late (as yearlings). Since body mass varies with age in immature animals of this species, I also examined possible effects of intruder body mass on responses by residents towards intruding males.

METHODS

Study population

I studied a population of *S. beldingi* in a 20 hectare alpine meadow from 31 May to 5 August 1999, 17 May to 8 August 2000, and 5 May to 20 August 2001 in the Sierra Nevada mountains at Tioga Pass in Mono County, CA. The study site has been described in detail by Sherman and Morton (1984). In *S. beldingi*, a four month active season during late spring and summer is followed by eight months of hibernation (Morton et al., 1974; Sherman and Morton, 1984). I defined individuals as juveniles if they were born during the current active season, and as yearlings if they were born the previous year. I trapped squirrels using tomahawk live-traps (Tomahawk Live-trap Co., Tomahawk, WI) baited with peanut butter, and released individuals at their original capture sites. At each capture, the squirrel's age, sex, reproductive condition, and trapping location were recorded. I also weighed individuals to the nearest 1g using spring balance scales (Avinet, Dryden, NY). Yearling and juvenile males were repeatedly trapped and weighed during the course of the study period.

Trapped individuals were marked with monel metal ear tags (National Band & Tag Co., Newport, KY) and fur dye (Nice'n Easy #124, Clairol Inc., Stamford, CT) to facilitate visual identification. I considered females to be reproductively active if they were either pregnant or lactating. I located and marked the nest burrow of each female by observing her activity during the breeding season. The breeding season included mating, gestation, and lactation periods, whereas the post-weaning period began when juveniles first emerged from their natal burrows at weaning, 25–28 days after birth (Holekamp, 1984b). I trapped and tagged all juveniles within 4 days of their first emergence above ground, during which time they remain within a few meters of their natal burrows and can be unambiguously assigned to a litter (Sherman, 1976). Based on the maximum size of a maternal territory at the time when litters are weaned, I defined a male's natal area as a circle with a 80 m radius centered on his natal burrow (Holekamp, 1984b). I considered an individual as having dispersed if he had permanently departed from his mother's territory, and if he was later consistently observed and trapped at least 80 m from his birth site. The dispersal history of all yearlings was known from this and earlier work (e.g., Nunes and Holekamp, 1996).

Staged Encounters

I performed one set of staged intruder experiments in 1999, and another in 2001, to compare responses by adult females towards tethered intruders ('stimulus animals') that were either juveniles or yearlings at the time of testing. In 1999, I conducted intruder experiments during the lactation period (26 June – 27 July 1999) using both male and female stimulus animals that were either juveniles or yearlings at the time of testing. These experiments allowed me to evaluate effects of sex and age of the stimulus animal on aggressive responses by lactating females towards intruders. I used as female stimulus animals only animals that were not yet reproductively active, as indicated by their small nipple size. In 2001, using only males as stimulus animals, I conducted additional intruder experiments during two different periods, the lactation period (21 June – 05 July 2001) and the post-weaning period (11 - 23 July 2001), to examine seasonal influences on responses of females towards male intruders. In each experiment, I tethered a single stimulus animal near the nest burrow entrance of an adult female conspecific, and then recorded events ensuing when the resident female encountered the tethered intruder.

I assigned each experimental female to one of two periods based on when her particular trial took place. Females lactating at the time of testing were assigned to the 'lactation period,' and experimental females that had already weaned their young of the year were assigned to the 'post-weaning period'. I trapped pregnant females frequently and estimated a female's parturition date based on when I observed a significant drop in body mass in conjunction with nipple enlargement. We used estimated parturition date as the criterion for selecting females as subjects for trials during the lactation period, and females were used approximately 14 days after they gave birth. I later calculated a more precise parturition date after each female weaned her litter by subtracting 27 days, the average length of the lactation interval in this species, from the date I first observed her litter above ground (Holekamp, 1984b). For two experimental females whose litters had died before weaning, I was unable to determine the number of days the females had been lactating at the time they were tested. For the remaining 39 lactation trials, experimental females had been lactating for an average of 16.46 days on the day of the trial. Post-weaning trials were conducted 10.67 days after litters were first observed above ground.

Each yearling stimulus animal was drawn from an area far from the test female's territory, and was therefore unfamiliar to her. Juvenile stimulus animals were trapped from a second *S. beldingi* population located 9 km east of Tioga Pass in Lee Vining Canyon (LVC). Holekamp (1983) describes this second site in detail. Reproductive events in LVC occurred 3-4 weeks ahead of those in our main study population because LVC was located almost 1000 m lower in elevation. Thus, litters from the LVC population emerged above ground approximately 3-4 weeks before litters from our main study site. By using stimulus animals from LVC population we were able to select large juveniles for our lactation trials, which allowed us to better match the body sizes of yearling and juvenile stimulus animals. Each experimental female (*n*=53) and each stimulus animal (*n*=50) was used in only one experimental trial, except for two yearling males and one yearling female that were each used twice as stimulus animals. Stimulus animals were captured one day prior to the trial and kept in a tent near the study site overnight. These animals were housed individually in cages (60 x 40 x 15 cm) containing cotton nest material and *ad lib* mouse chow and water. Each stimulus animal was randomly assigned to an experimental female the next morning. The body mass of each stimulus animal was measured immediately after the trial and was returned to and released at its capture site.

The morning of the trial, I captured the experimental female and briefly removed her from the immediate vicinity of her nest burrow to avoid any premature exposure to the stimulus animal. I attached to the stimulus animal a harness made of light nylon line, similar in design to the harness developed by (Bakker et al., 1994). I then tethered the stimulus animal to a stake placed one meter downwind of the entrance of the experimental female's nest burrow. The tether consisted of a string permitting the animal to move within a circle of 50 cm diameter around the concealed stake to which the tether was attached. The experimental female was then released directly into her burrow and her behavior was recorded for 10 minutes, starting when she re-emerged and clearly detected the stimulus animal, as indicated by orienting her head and body towards it. Before and after the trial we carefully examined each stimulus animal to determine whether it had received any wounds during the trial, but I never observed any injuries being inflicted during any of the experimental trials.

I used the ethogram for Belding's ground squirrels developed by Holekamp (1983), and defined aggressive behavior by each experimental female as threatening, lunging at, or fighting with the stimulus animal. I recorded all aggressive behaviors directed by the female toward the stimulus animal during each trial. Each female was assigned an aggression intensity score based on the highest intensity of aggression she directed towards the stimulus animal: a female received a score of 0 if she showed no aggressive behavior, a score of 1 if she only threatened the stimulus animal, a score of 2 if she lunged at the stimulus animal, or a score of 3 if she initiated a fight with the tethered animal during the trial. I assessed the likelihood of experimental females aggressing against stimulus animals drawn from each sex and age group based on the proportion of trials during which females were observed to aggress against stimulus animals. I used the number of times a female emitted aggressive behaviors during the 10 min trial to calculate the rate at which the behavior was emitted per minute. I evaluated the propensity of females to aggress against stimulus animals, and the rates and intensities of their aggressive behavior, based on the sex and age of stimulus animals, and on whether trials were conducted during lactation or post-weaning periods.

Naturally-occurring encounters

In 2001, I conducted focal animal observations (Altmann, 1974) on free-ranging juvenile and yearling male intruders to evaluate responses by adult resident males and females towards these intruders in the context of naturally-occurring encounters. Behavioral observations were conducted between 0800 and 1900 hours Pacific daylight time, and I conducted 59 focal animal surveys during which I observed 10 yearling and 11 juvenile focal males for an average of 32.30 (±1.87) minutes during each survey. Focal animal observations of yearling males were conducted both during the breeding season and during the post-weaning period. Juvenile males were only observed during the post-weaning period, which was the earliest I observed them venturing away from their natal areas, approximately 2 weeks after their initial emergence from the natal burrow. Juvenile males were observed outside of their natal areas between 31 July and 12 August 2001. Yearling males were observed between 6 June and 13 August 2001 in areas at least 80 m away from their sleeping burrows, and outside of their natal areas. Yearling males whose ages at dispersal were known could be classified as either 'early' or 'late' dispersers. 'Early' dispersers were yearlings that had dispersed at 7-10 weeks of age, and 'late' dispersers were yearlings that had dispersed at 51-55 weeks of age. We radio-collared (SOM-2190 transmitters, AVM Instrument Company, Ltd., Colfax, CA) most males, which allowed us to locate individuals regularly during exploratory forays. All yearling males and 9 of the 11 juvenile males wore radio-collars during the observation period.

During each focal animal survey, I recorded all cases in which a focal animal encountered another squirrel. I defined an encounter as a focal and non-focal squirrel coming within 20 m of each other, regardless of whether an interaction occurred between the squirrels. When an encounter occurred, I recorded the identity of the encountered squirrel and the behavior of the resident squirrel towards the intruding male. I considered an interaction to occur during an encounter when the two animals came within 1 m of each other or when one of the squirrels clearly changed its behavior in response to the presence of the other squirrel by either orienting to or approaching it. When an interaction occurred, it was identified as aggressive or non-aggressive. That is, in an aggressive interaction a non-focal animal threatened and/or chased a focal animal, whereas during a non-aggressive interaction a conspecific came within 1 m of the focal animal but showed no signs of aggression.

From focal animal data, I calculated hourly encounter rates at which intruding focal males came within 20 m of adult male and female residents. Adults were considered to be residents of a particular area if they were known to sleep in burrows there. A focal male's encounter rate with adult residents of one sex was its total number of encounters with adults of that sex divided by the total number of hours that focal animal was observed. Because early dispersers leave home during the post-weaning period whereas late dispersers leave home during the breeding season, I compared rates of encounters between residents and juveniles during the post-weaning season with encounter rates between residents and yearlings during the breeding season. I also compared rates of encounters of yearling male focal animals and adult residents of each sex between breeding and post-weaning seasons.

Because intraspecifc aggression is common in *S. beldingi* during the breeding season when late dispersers emigrate, but rare when early dispersers leave home after weaning, I predicted that local residents would be more likely to aggress against late than early dispersers during immigration. To test this prediction I compared probabilities of experiencing aggression from resident adults between juvenile focal males when they dispersed during the post-breeding season and yearling focal males when they dispersed during the breeding season. For this comparison, I only included yearling male focal data collected during the breeding season but all juvenile focal data, since juvenile males were only observed during the post-weaning period. I examined seasonal influences on resident responses towards yearling intruders by comparing breeding and post-weaning seasons with respect to the probability of adult residents of both sexes aggressing against yearling focal males. In addition, I also performed pair-wise comparisons of male and female responses towards focal males to determine whether aggressive tendencies differed between male and female adult residents. Finally, I examined encounter rates of yearling males and responses of residents towards these males based on yearling male dispersal history. That is, I evaluated the rates of encounters by yearlings with residents of each sex, as well as the probability of experiencing aggression from residents during encounters, based on whether the yearling males had dispersed early or late.

Analysis of body mass

The body mass of male *S. beldingi* varies with age, so resident animals may perceive large intruders as a greater threat than small intruders, independent of intruder age, and modulate their aggressive responses accordingly. Although I attempted to select subject animals of similar body size within each age group, I also performed several analyses to systematically compare body mass among: early and late dispersers at the time of dispersal, stimulus males tested in tethering experiments, and males watched as focal animals. I also compared the body mass of focal and stimulus males within each age group (e.g., juvenile focal vs. juvenile stimulus animals), and I compared body mass between age groups within sampling groups (e.g., juvenile focal vs. yearling focal animals). Body mass at dispersal was estimated for 'early' (*n*=62) and 'late' dispersers (*n*=18) between 1993 and 1997 by trapping dispersers within 10 days of their settlement in new areas after emigration from their natal sites. Body mass of each stimulus animal was obtained on the day of its tethering trial. Yearling focal males were weighed on average 7.7 (±0.56) times during the period in which we observed them, so I calculated a mean body mass for each focal yearling during the observation period. Most juvenile focal males were weighed only once during the observation period, with the exception of two males that were each weighed three times. For each of these two males, I calculated a mean body mass for the observation period. One juvenile focal male was not weighed during the observation period, and was therefore not included in the body mass analysis. On average, yearling males were weighed within 10.4 (±1.64) days and juvenile males 3.6 (±1.64) days of the dates they were observed.

Statistical Analyses

Since rates and intensities of aggression emitted by experimental females in intruder experiments were not normally distributed (Lilliefors test, $P<0.05$), I used Mann-Whitney U tests to assess these measures. Similarly, naturally-occurring encounter rates between residents and yearling males grouped on the basis of dispersal age were not normally distributed, so we used Mann-Whitney U tests to compare encounter rates between early and late dispersers observed as yearlings. To assess naturally-occurring encounter rates between focal males and residents, I used a two-way ANOVA to examine effects of resident sex (male vs. female) and current age (juvenile vs. yearling) of the focal animal. Chi-square tests and two-tailed Fisher exact tests were used to evaluate the probability of aggression occurring during staged and naturally-occurring encounters. I used a t-test to evaluate differences in body mass among male and female juvenile and among male and female yearling stimulus animals used for lactation trials. I also used a t-test to compare the mean body mass of juveniles and yearlings within each subject group (disperser, stimulus animal, or focal animal). For males in each age group, we used a one-way ANOVA to determine whether body mass varied among dispersers, stimulus animals, and focal animals. I further divided yearling male focal animals into early and late dispersal groups for this analysis. Differences among groups were considered significant when $P<0.05$. I adjusted significance levels of multiple pair-wise comparisons using the Bonferroni correction. All statistical tests are described in (Sokal and Rohlf, 1995). Rates of behavior are presented as means ±*SE*.

RESULTS

Staged Encounters

In 1999, I conducted 30 staged intruder experiments during the lactation period using seven juvenile females, seven yearling females, eight juvenile males, and eight yearling males as stimulus animals. In 2001, I conducted 11 additional experiments during the lactation period with five juvenile and six yearling stimulus males, and 12 experiments during the post-weaning period with six juvenile and six yearling stimulus males. I combined data from lactation trials conducted with male stimulus animals in 1999 and 2001 because I observed no differences between years with respect to aggression emitted by experimental females (towards juvenile males: threat: $U = 25.00$, $P = 0.245$, fight: $U = 20.50$, $P = 0.921$, aggression intensity scores: $U = 25.00$, $P = 0.401$; towards yearling males: threat: $U = 37.50$, $P = 0.076$, fight: $U = 22.50$, $P = 0.842$, aggression intensity scores: $U = 25.00$, $P = 0.880$).

Lactating females were equally likely to aggress against males and females when juvenile stimulus animals were tethered ($\chi^2 = 0.20$, *df* = 1, $P = 0.658$; Fig. 1). Lactating females tended to be more likely to aggress against yearling males than yearling females, but this difference was not statistically significant ($\chi^2 = 2.68$, *df* = 1, $P = 0.102$). Lactating females were no more likely to aggress against yearling than juvenile females (Fisher exact test, $p = 1.00$), but were significantly more likely to aggress against yearling than juvenile males ($\chi^2 = 4.49$, *df* = 1, $P = 0.034$).

Sex of stimulus animal did not appear to influence rate or intensity of aggression directed by experimental females towards tethered juveniles (Fig. 2). Lactating females threatened and fought with juvenile male and female stimulus animals at similar rates, and with similar intensity scores (threat: $U = 45.00$, $P = 0.949$, fight: $U = 45.00$, $P = 0.958$, intensity score: $U = 48.00$, $P = 0.814$; Fig. 2). I also observed no significant differences between yearling males and yearling females with respect to rate or intensity of aggression experimental females directed at them (threat: $U = 71.00$, $P = 0.086$, fight: $U = 60.50$, $P = 0.370$, intensity score: $U = 63.5$, $P = 0.220$).

Aggressive responses of lactating females varied with age of the tethered stimulus animal. Experimental females tended to direct higher rates and intensities of aggression towards yearling than juvenile stimulus animals of both sexes (Fig. 2), but this tendency was only statistically significant among male stimulus animals (juvenile females vs. yearling females: threat: $U = 21.00$, $P = 0.534$, fight: $U = 18.0$, P=0.332, aggression intensity scores: U=21.00, P=0.591;

juvenile male vs. yearling male: threat: U=36.50, P=0.004, fight: U=43.50, P=0.011, aggression intensity scores: U=49.50, P=0.028).

The seasonal comparison of aggressive tendencies of females showed that experimental females were just as likely to aggress against juvenile males (χ^2=0.05, df=1, P=0.830) or yearling males (χ^2=1.63, df=1, P=0.201) during both test periods. Whereas male age influenced the probability experimental females directed aggression towards intruders in trials conducted during the lactation period (Fig. 1), this age effect was not observed in post-weaning trials. During post-weaning trials, experimental females were equally likely to show aggression towards juvenile and yearling males (Fisher exact test, P=1.00).

Aggression rates and intensity scores of experimental females were similar for juvenile males between lactation and post-weaning trials (threat: U=45.00, P=0.324, fight: U=48.0, P=0.214, intensity score: U=48.50, P=0.311; Fig. 3). In contrast, lactating females showed significantly higher rates of aggressive behavior, and received higher intensity scores, during their interactions with yearling male stimulus animals than did females used in post-weaning trials (threat: U=66.00, P=0.037, fight: U=66.00, P=0.034, intensity score: U=64.50, P=0.042). During post-weaning trials, rates and intensities of aggression by experimental females did not differ between juvenile and yearling males (threat: U=15.00, P=0.317, fight: U=15.00, P=0.317, intensity score: U=15.00, P=0.528).

Naturally-occurring encounters between focal males and resident adults

I observed 11 juvenile males for an average of 1.03 h (±0.21) during which we recorded 17 naturally-occurring encounters with resident females and 14 encounters with resident males. I also observed 10 yearling males, including five males that had dispersed early and five that had dispersed late, for an average of 2.11 h (±0.46) during which we recorded 67 encounters with resident females, and 27 encounters with resident males. Yearlings that had dispersed early were observed on average for 2.36 h (±0.82), and yearlings that had dispersed late for 1.86 h (±0.52). I conducted focal animal surveys on nine of the 10 yearling males during the breeding season (1.56 ±0.82 h/male) and on seven of the 10 yearling males during the post-breeding season (1.01 h ±0.33 h/male). Only six of the 10 yearling males were observed during both seasons.

Rates at which focal animals came within 20 m of male and female residents varied significantly overall ($F_{1,48}$=58.63, P< 0.000; Fig. 4a). Focal males encountered male residents at significantly higher rates than they encountered female residents ($F_{1,48}$= 4.81, p = 0.033). However, encounter rates with residents did not differ significantly between juvenile and yearling focal males ($F_{1,48}$=0.42, P=0.659), and I observed no interaction effect between focal animal age and sex of resident on encounter rates ($F_{2,48}$=0.68, P=0.510). Since juvenile males did not begin making forays out of their natal areas until the post-weaning period, this analysis did not include encounter rates of juveniles collected during the breeding season. Yearling males that had dispersed late tended to encounter male residents at higher rates than female residents (Z=1.83, P=0.068; Fig. 4b), but I observed no such pattern for yearlings that had dispersed early (*Z*=1.46, *P*=0.144). Encounter rates with female residents did not differ significantly between early and late dispersers (*U*=9.50, *P*=0.531), but late dispersers tended to encounter male residents at higher rates than did early dispersers (*U*=4.00, *P*=0.076). All interactions (*n*=22) between yearling focal animals with adult male and female residents were aggressive in nature as were 71% (*n*=5) of interactions between juvenile focal animals and adult male and female residents.

Intruder age influenced responses by female but not male residents towards focal males during encounters. Adult female residents were significantly more likely to aggress against yearling focal males they encountered during the breeding season than against juvenile focal males they encountered during the post-weaning period (χ^2=3.96, *df*=1, *P*=0.047; Fig. 5a). Adult males residents, however, were just as likely to aggress against yearling males they encountered during the breeding season as against juvenile males they encountered during the post-weaning period (χ^2=0.01, *df*=1, *P*=0.919; Fig. 5b).

The seasonal comparison of aggressive responses by residents during encounters with yearling focal males showed that the likelihood of residents aggressing against focal yearlings tended to be higher during the breeding season than the post-weaning period. However, this seasonal difference in resident behavior towards yearling intruders was only statistically significant for female residents (female residents: χ^2=7.22, df=1, *P*=0.007, Fig. 5a; male residents: χ^2=1.36, df=1, *P*=0.244, Fig. 5b). During the post-weaning period, male and female residents were equally likely to aggress against juvenile males during encounters (χ^2=0.46, df=1, P=0.497). I also observed no significant differences between aggressive tendencies of male and female residents towards yearling males during either the breeding season (χ^2=0.99, df=1, P=0.320) or the post-weaning period (χ^2=0.01, df=1, P=0.923).

Although both early and late dispersers were observed simultaneously, female residents were significantly more likely to aggress against focal yearlings that had dispersed late than against those that had dispersed early (χ^2=8.89, df=1, P=0.003; Fig. 6). In contrast, male residents were equally likely to aggress against yearlings in both groups (χ^2=0.48, df=1, P=0.488). Male residents and female residents were equally likely to aggress against early dispersers during encounters (χ^2=0.50, df=1, P=0.481). Female residents, however, were significantly more likely than male residents to aggress against late dispersers (χ^2=4.33, df=1, P=0.038). These data suggest that the age at which a yearling male dispersed influences aggressive responses by female but not male residents towards focal males during naturally-occurring intrusion events.

Body mass comparison

I observed marked variation among the body masses of the various subject groups of juvenile and yearling males (juvenile males: $F_{2,88}$=5.88, P=0.004; yearling males: $F_{3,44}$=8.08, P<0.001; Fig. 7). Juvenile focal males were significantly lighter than juvenile males at the time of dispersal ($t_{1,70}$ =3.63, P<0.001). The body mass of juvenile stimulus males did not differ significantly from that of either juvenile focal males ($t_{1,70}$=1.34, P=0.192) or juvenile dispersers at the time of dispersal ($t_{1,79}$=1.74, P=0.085). Yearling stimulus males and yearling focal males of both dispersal age groups were significantly heavier than yearling dispersers at the time of emigration, even after Bonferroni correction (dispersal vs. stimulus: $t_{1,36}$ =3.65, P=0.001, $\alpha_{adj.}$= 0.013; dispersal vs. early focal: $t_{1,21}$=3.90, P=0.001, $\alpha_{adj.}$=0.01; dispersal vs. late focal: $t_{1,21}$=3.13, P=0.005, $\alpha_{adj.}$=0.017). Yearling focal and stimulus males did not differ significantly in body mass (stimulus vs. early focal: $t_{1,23}$ =1.700, P=0.103, $\alpha_{adj.}$= 0.025; stimulus vs. late focal: $t_{1,23}$=1.04, P=0.307, $\alpha_{adj.}$=0.05). Yearling males in each male category were significantly heavier than juvenile males in the same categories (dispersal: $t_{1,78}$=2.06, P=0.042, stimulus: $t_{1,37}$=5.18, P<0.001; focal: $t_{1,18}$=9.31, P<0.001). We observed no significant sex difference in body mass among male and female juvenile stimulus animals used for lactation trials ($t_{1,18}$ =1.46, P=0.161). However, yearling males stimulus animals were significantly heavier than their female counterparts ($t_{1,19}$ =3.27, P=0.004)

Despite my best efforts to equalize their body masses, yearling subject animals were consistently heavier than juvenile subjects. Therefore, I performed two post-hoc comparisons to inquire whether aggressive responses of female residents varied with intruder body mass rather than with intruder age. First, I used regression analysis to determine whether there was a relationship between stimulus male body mass and observed female behavior during lactation trials. For theses analyses, I used the body mass of stimulus males as the independent variable, and aggression rates and intensities emitted by lactating females as dependent measures. I found that stimulus animal body mass explained less than 4% of the observed variance in female aggression towards males for all three measures of aggression (threat: R^2=0.03; fight: R^2 = 0.01; intensity scores: R^2=0.04). Furthermore, no relationship between stimulus male mass and any measure of female aggression towards stimulus males was statistically significant (threat: $F_{1,25}$=0.82, P=0.374; fight: $F_{1,25}$=0.21, P=0.651; intensity score: $F_{1,25}$=1.03, P=0.320). Second, I compared the mean body mass of yearling focal males that had dispersed early to that of yearling focal males that had dispersed late. Although resident females were significantly more likely to aggress against late than early yearling males (Fig. 6), body mass of focal yearlings did not differ between early and late dispersers ($t_{1,9}$=0.61, P=0.557). These results suggest that aggressive responses of resident females towards intruding males are not determined by intruder body mass.

DISCUSSION

In the Belding's ground squirrel, intruder age significantly influenced aggressive responses by resident females towards intruding males during both tethering experiments and naturally-occurring encounters. Lactating females were more likely to aggress against, and directed higher rates and intensities of aggression towards, yearling than juvenile males, although these differences disappeared after the breeding season ended. Intruders in both age groups were more likely to encounter adult resident males than resident females, but resident females were far more aggressive to intruders than were male residents, particularly to yearling intruders. Adult male residents were equally likely to aggress against juvenile and yearling male intruders. These findings are consistent with previous accounts of social interactions reported for this species. For example, Sherman (1976) observed that 83% of encounters between female residents and yearling male immigrants lead to yearlings being chased by adult females. In addition, Holekamp (1983) noted that 91% of observed interactions between yearling males and unrelated adults involved adult females, whereas only 9% occurred between yearlings and adult males. Considering that all adult-yearling interactions we observed were aggressive in nature, Holekamp's data are consistent with our observation that yearling males are primarily targeted for aggression by adult females. Thus, by dispersing as juveniles, males searching for a new home appear to avoid aggression from female residents.

Variation in female responses towards intruders reflects variation in infanticidal tendencies among various types of intruders. Infanticide is common in this species, and territorial aggression by female *S. beldingi* throughout the breeding season helps them defend their young from infanticidal conspecifics (Nunes et al., 2000; Sherman, 1976). Yearling male immigrants have been observed to commit about one third of observed infanticides, whereas non-reproductive yearling females have rarely, and juvenile males and females have never, been observed killing infants (Sherman, 1981b). Here, we found that aggressive responses of experimental females during lactation trials were greatest towards yearling males, intermediate towards yearling females, and lowest towards juveniles of both sexes (Figures1 & 2). Differential treatment by experimental females of juvenile and yearling stimulus males ceased after young were weaned, when pups were mature enough to flee and defend themselves from conspecifics. In mammalian species where immigrants commit infanticide, the need to protect young from such intruders has been invoked to explain female aggression toward immigrant males (Agrell et al., 1998). Female aggression may be most effective for excluding immigrants in species where males and females are relatively monomorphic as in *S. beldingi*, and males are not able to use larger body size to overcome aggression by female residents. Hence, the need to avoid female aggression may have been an especially important selection pressure shaping age of dispersal in such mammals.

In *S. beldingi*, adult male aggression peaks during the breeding season, when adult males actively compete for mates, and subsequently drops to its lowest levels as males begin fattening for hibernation (Sherman, 1976). I therefore predicted that adult male residents would be more likely to aggress against yearling males intruding during the breeding season than against juveniles intruding during the post-weaning period. However, aggression by resident males towards yearling intruders was relatively uncommon, and the proportion of interactions between adult and yearling males that were aggressive was only slightly higher during the breeding season than during the post-weaning period. Similarly, Sherman (1976) found significantly fewer wounds from male combat on yearling than older male *S. beldingi* during the breeding season. The relatively low frequency of adult aggression towards yearling males suggests that adult males do not indiscriminately target potential competitors, but rather appear to direct their aggression selectively based on the reproductive status and competitive ability of other males. This may also be true in European ground squirrels, *S. citellus*, in which only 11.4% of male-male aggression observed during the mating period occurs between adult males and immature yearling males (Millesi et al., 1998). In *S. beldingi*, immature males pose little threat to the future reproductive success of adult resident males because male mortality is high across all ages, and there is only a small chance that an adult male will later compete with males he once encountered as immature individuals (Sherman and Morton, 1984).

In addition to *S. beldingi*, juvenile dispersal coincides with reduced resident aggression in a number of other ground-dwelling sciurids. Resident aggression towards juvenile immigrants has only been documented in two of the 13 species showing predominant juvenile dispersal. In the Uinta ground squirrel, *S. armatus*, adult males aggressively target juvenile males during the post-weaning period and this aggression appears to reduce the likelihood of the immigrants becoming sexually mature as yearlings (Slade and Balph, 1974). Suitable hibernation sites are scarce in the Arctic ground squirrel, *S. parryii*, and adult males and females aggressively defend territories surrounding their hibernacula during the post-weaning period from other conspecifics, including juvenile immigrants (Carl, 1971). Interestingly, both early and late dispersing *S. columbianus* males appear to avoid resident aggression by dispersing towards the end of the species' active season when resident aggression is low (Waterman, 1992; Wiggett and Boag, 1993). In most prairie dog (black-tailed prairie dog, *C. ludvicanus*; Gunnison's prairie dog, *C. gunnisoni*) and marmot species (*M. flaviventris*; hoary marmot, *M. caligata*; golden marmot, *M. caudata aurea*; Alpine marmot, *M. marmota*; Olympic marmot, *M. olympus*) the resident male or all members of a social group aggressively defend a territory throughout the species' active season, and early dispersal therefore does not reduce resident aggression towards prospective immigrants (Armitage and Downhower, 1974; Barash, 1973; Blumstein and Arnold, 1998; Garrett and Franklin, 1988; Hoogland, 1999; Michener, 1979a; Michener, 1979b). Hence, in species where territorial defense tends to be continuous, males may benefit from delaying dispersal until they are larger and have greater chances of immigrating successfully. However, lack of tolerance by local residents towards immature males may make it impossible for males to delay emigration until a time when immigration prospects are optimal. This appears to be the case in *S. parryii* where juvenile males are evicted by their mothers (Carl, 1971). Although, the timing of dispersal in other ground squirrel species relative to seasonal fluctuations in resident aggression supports the hypothesis that early dispersal reduces social resistance encountered by immigrant males, our results must be interpreted cautiously. A more rigorous comparative approach and the inclusion of other characters, such as body size, are necessary to assure independence among data points (Harvey and Page, 1991) and to assess the importance of other variables in the evolution of dispersal age in these species (Armitage, 1981; Barash, 1974).

In our study, intruder age rather than intruder body mass appeared to influence aggressive responses by resident females. However, age and body size tend to be highly correlated in mammals, and the combination of age and competitive ability, rather than age alone, may affect immigration patterns in some species. For example, in both Japanese macaques (*Macaca fuscata*) and savannah baboons (*Papio cynophalus)*, reproductive potential of males is highest when they are physically and socially at their prime, but the timing of dispersal relative to this prime differs between the species, as does the relative size and age at which males disperse. Male savannah baboons emigrate shortly after reaching adult body size, and tend to rise quickly to the top of the dominance hierarchy in the new troop (Alberts and Altmann, 1995). In contrast, male Japanese macaques disperse when they are not yet fully grown, and enter the new troop at the bottom of the hierarchy (reviewed by (Sprague, 1992). In meerkats, *Suricata suricatta*, and dwarf mongoose, *Helogale parvula*, males that immigrate into a pack as subadults do so as subordinate non-breeders, whereas males that disperse once they are near or at adult size can attain breeding status if they can able to aggressively oust the dominant male(s) (Doolan and Macdonald, 1996; Rood, 1987). In many mammals, dispersers often exhibit specific behaviors that allow them to minimize aggression from residents. For example, dispersers may try to avoid residents by being silent and inconspicuous while traversing or entering foreign habitat (e.g., red squirrels, *Tamiasciurus hudsonicus*, Larsen and Boutin, 1994; gibbons, *Hylobates lar*, Brockelman et al., 1998).

Although the adult sex ratio is female-biased in our *S. beldingi* study population (Sherman and Morton 1982, Muecke and Nunes unpublished data), intruding males encountered resident males at significantly higher rates than resident females. Males thus appeared to minimize conflict by avoiding female residents. Sherman (1977) observed that adult and immigrant yearling male *S. beldingi* tend to limit their activity to areas between female breeding sites or to areas of low female density. Similar observations have been made for other sciurid species. For example, in Richardson's ground squirrels, *S. richardsonii* (Michener, 1979a), and *S. columbianus* (Murie and Harris, 1978), adult and yearling males are either absent from, or occupy areas peripheral to, female nesting sites. In addition, *S. beldingi* yearlings may also avoid female aggression by altering their activity schedule to minimize temporal overlap with territorial females. This was suggested by Sherman (1976), who reported that immigrant males with sleeping burrows on or adjacent to female territories delay or advance their entry and exit from their sleeping burrows to avoid the resident females. We observed similar movement and activity patterns among yearling males here, and we also noted that males on exploratory excursions tended to utilize non-breeding areas as travel routes. Hence, it appears that by avoiding females in time and space, male *S. beldingi* are able to reduce the likelihood of encountering aggression by female residents during exploratory excursions.

Here the age at which males dispersed influenced their behavior as yearlings as well as the responses directed by female residents towards them as yearlings. Yearling males that had dispersed late tended to encounter male residents at higher rates than female residents, and also tended to have higher encounter rates with male residents than did yearlings that had dispersed early.

During encounters with female residents, these males were also significantly more likely to be targets of aggression than were early dispersers. Familiarity with intruders can reduce aggressive responses by residents (French et al., 1995), and repeated intrusions by the same individual into a territory might tend to reduce aggressive responses by the resident towards the intruder (Switzer et al., 2001). The relatively higher male than female encounter rates of late dispersers suggest that late dispersers tend to intrude less frequently into areas that are occupied by females, which appears to influence how these yearlings are treated by resident females. Hence, age at the time of dispersal has significant social consequences for males that extend beyond the dispersal period and perhaps even persist into adulthood. Familiarity with a male's odor increases sexual behavior of female golden hamster, *Mesocritecus auratus*, during mating trials (Tang-Martinez et al., 1993), and female giant kangaroo rats, *Dipodomys ingens*, prefer to mate with familiar males (Randall et al., 2002). *S. beldingi* males roam widely in their search for receptive mates, and if familiarity plays a similar role in female mate choice in this species, early dispersal may allow males to introduce themselves to females as prospective mates, and subsequently enhances their own mating success. This might offer an additional ultimate explanation for why early dispersal predominates in this species. However, overall our results support the hypothesis that juvenile dispersal is adaptive for male *S. beldingi* by allowing male immigrants to avoid aggression from local residents. Aggression by residents towards immigrants has been observed in many mammals, and this aggression can influence immigration patterns (Brandt, 1992). The need to avoid resident aggression may thus also affect age at dispersal of other mammals.

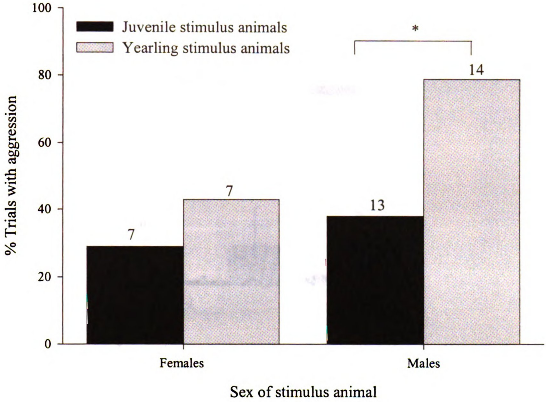

Figure 1: Percent of 10-min trials during which experimental females aggressed against tethered stimulus animals. All trials shown here took place during the lactation period. Sample sizes above bars refer to the total number of trials conducted for each stimulus animal group. Horizontal bar with asterisk indicates that groups differ significantly at $P < 0.05$.

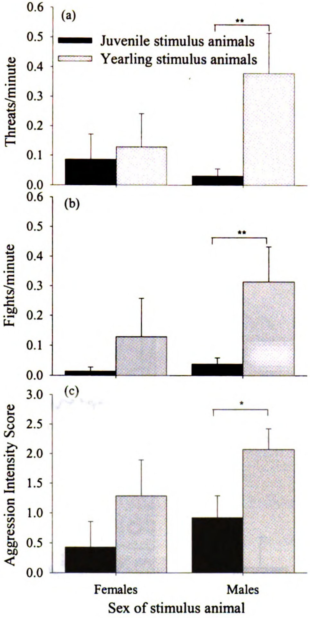

Figure 2: Mean rates of threat (a), rates of fighting behavior (b), and aggression intensity scores (c) directed by experimental females towards juvenile female (*n* = 7), juvenile male (*n* = 13), yearling female (*n* = 7), and yearling male (*n* = 14) stimulus animals. All trials shown here took place during the lactation period. Asterisk indicates significant differences between groups at *P*<0.05 and double asterisks indicate *P* < 0.01.

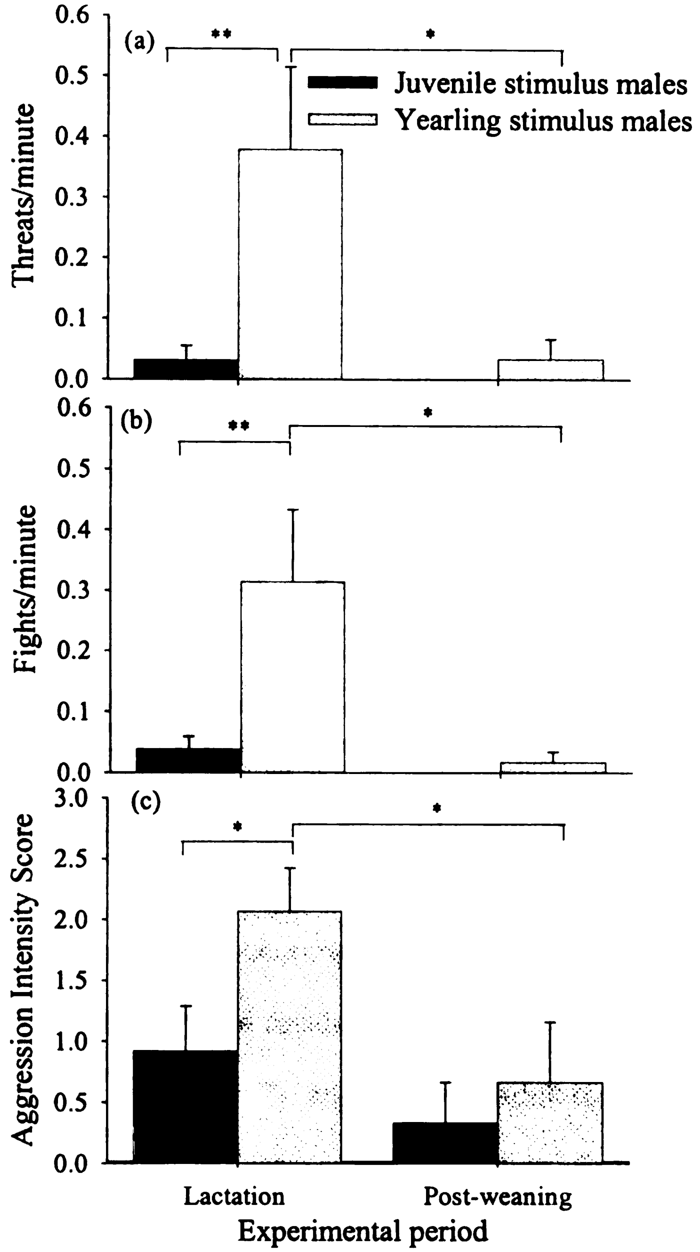

Figure 3: Mean rates of threat (a), rates of fighting behavior (b), and aggression intensity scores (c) directed by experimental females towards tethered juvenile males (*n* = 13) and yearling males (*n* = 14) during lactation trials and towards juvenile males (*n* = 6) and yearling males (*n* = 6) during post-weaning trials. Other notation is as in figure 2.

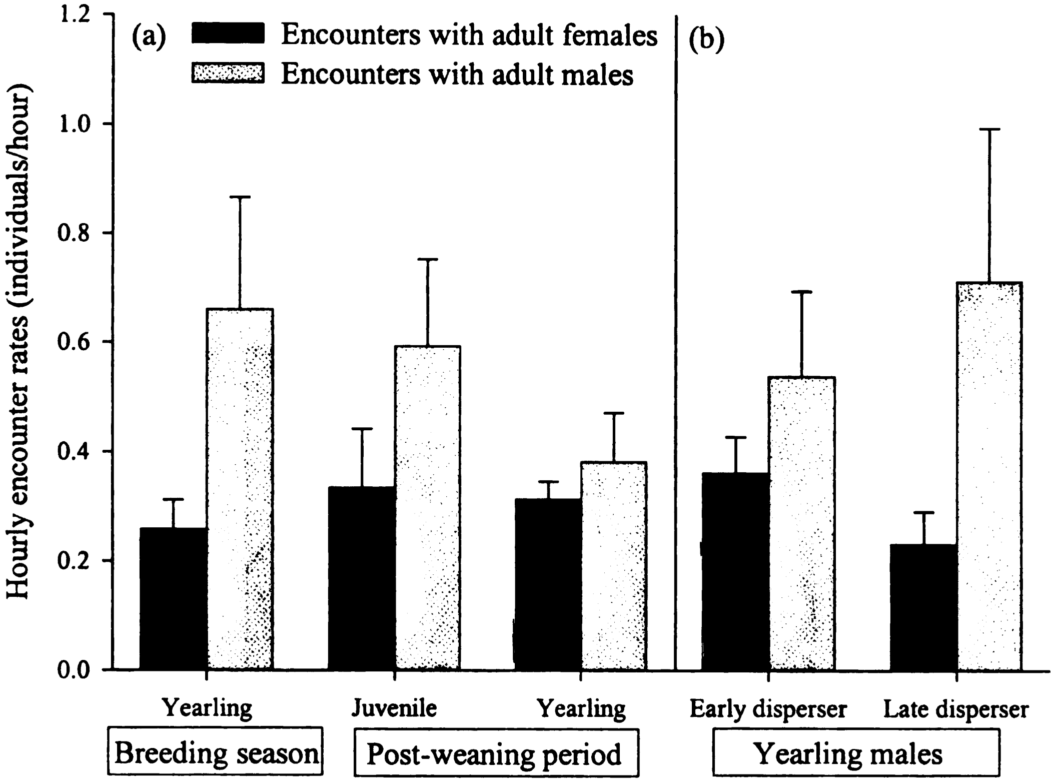

Figure 4: (a) Rates of naturally-occurring encounters between yearling focal males and adult male and female residents during the breeding season (*n*=9) and the post-weaning period (n = 7), and between adult residents and juvenile focal males (*n* = 11) during the post-weaning period. (b) Rates of encounters with adult resident by yearling males that had dispersed either as juveniles (early dispersers, *n* = 5) or as yearlings (late dispersers, *n* = 5). Data in (a) but not (b) are normally distributed, so data shown in a & b cannot be directly compared.

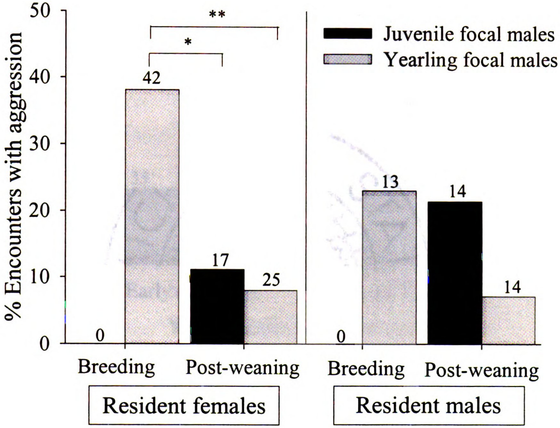

Figure 5: Aggressive behavior directed by female (a) and male (b) residents towards juvenile (*n* = 11) and yearling (*n* = 10) male focal animals during naturally-occurring encounters. Sample sizes above bars refer to the total number of encounters observed for each focal male subject group. Other notation is as in Figure 2.

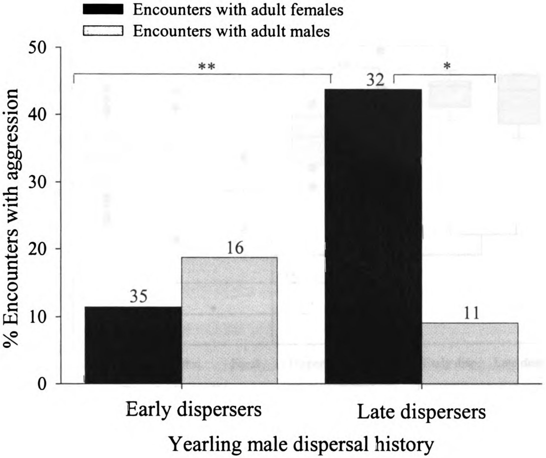

Figure 6: Aggressive behavior directed by adult male and female residents towards yearling focal males that had dispersed either as juveniles (early dispersers, *n* = 5) or as yearlings (late dispersers, *n* = 5). Sample sizes above the bars refer to the total number of naturally-occurring encounters we observed involving males from each yearling group. Other notation is as in Figure 2.

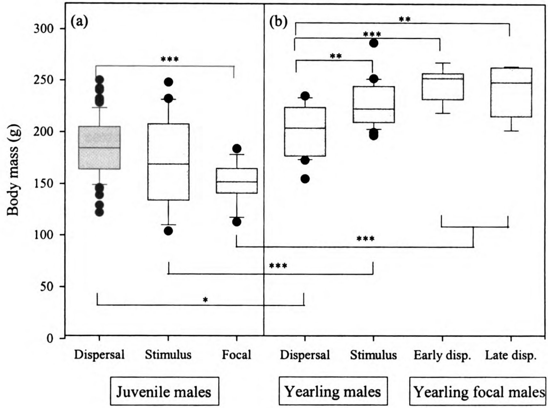

Figure 7: (a) Body mass of juvenile males (*n* = 62) at the time of dispersal, juvenile stimulus males (n = 19) on the day of the experimental trial, and juvenile focal males (*n* = 10) during the post-weaning period. (b) Body mass of yearling males (*n* = 18) at the time of dispersal, yearling stimulus males (*n* = 20) on the day of the trial, and yearling focal males that had dispersed either as juveniles (early dispersers, *n* = 5) or as yearlings (late dispersers, *n* = 5). Body mass of focal males weighed more than once per observation period was averaged for this comparison. Triple asterisks indicate significant differences at *P* < 0.001. Other notation is as in Figure 2.

CHAPTER THREE

EARLY DISPERSAL DOES NOT IMPROVE SURVIVORSHIP BUT IS CORRELATED WITH ENHANCED MATING SUCCESS AMONG MALE BELDING'S GROUND SQUIRRELS (*SPERMOPHILUS BELDINGI*)

INTRODUCTION

Natal dispersal, the permanent departure of an individual from its birthplace, is sexually dimorphic in most mammals, with males dispersing while females remain at their birth site throughout their lives (Greenwood, 1980; Lidicker, 1975). Dispersal represents one of the most profound environmental changes an individual is likely to experience during its lifetime. A disperser leaves behind the safety of a familiar social and physical environment, and must navigate through unfamiliar habitat where he is exposed to many mortality factors such as predation and lack of essential resources. After he has located a suitable habitat, the emigrant must rapidly assimilate knowledge about the social and physical features of his new home to ensure successful settlement (Isbell and Van Vuren, 1996; Van Vuren and Armitage, 1994; Waser and Jones, 1983a). The costs of dispersal can be substantial and may include exclusion from important resources (Garrett and Franklin, 1988), loss of reproductive opportunities (Alberts and Altmann, 1995), injury, and even death (Byrom and Krebs, 1999; Larsen and Boutin, 1994). In mammals, natal dispersal often occurs before individuals reach sexual maturity (Dobson, 1982), yet because of their small body size and inexperience, young emigrants may be particularly vulnerable to risks associated with dispersal. This apparent paradox suggests that dispersal age has a strong impact on male fitness. Despite the fact that considerable anecdotal evidence in the literature supports this notion, few studies have evaluated the effect of age at dispersal on male fitness.

My objective here is to assess the influence of dispersal age on male fitness in Belding's ground squirrels (*Spermophilus beldingi*). Dispersal behavior has been studied extensively in this species, which exhibits the male-biased pattern of emigration typical of most mammals. *S. beldingi* are diurnal, easily trapped and observed, and individuals can be followed throughout most of the reproductive lifespan. In addition, the reproductive and social behavior of this species has been described in detail, providing the necessary foundation on which to evaluate male fitness. In *S. beldingi*, a four-month active season is followed each year by eight months of hibernation (Morton et al., 1974; Sherman and Morton, 1984). Although approximately 70 - 90 % of dispersers emigrate as juveniles (early dispersers), 10 - 30 % depart the following summer as yearlings (late dispersers), and all males leave home before they are 55 weeks old (Holekamp, 1986). Juvenile dispersers typically leave their natal site when they are 7 – 10 weeks old and weigh only 183 g (Nunes and Holekamp, 1996). Yearling dispersers are roughly one year old and weigh 250 g (Chapter 2). Mortality is high throughout a male's lifespan, and a male has a less than 50% chance of surviving from one year to the next (Sherman and Morton, 1984). Males become reproductively mature at age two. *S. beldingi* are highly polygynous, and reproductive success is highly skewed among adult males (Sherman 1976).

Considering the persistent bias towards early dispersal and a male's limited prospects for survival and reproduction it is likely that selection has favored juvenile dispersal in Belding's ground squirrels because males that disperses early gain significant fitness benefits over males that disperse as yearlings. Here, I test predictions of this hypothesis using extensive live-trapping and observations of matings to evaluate the effects of age at dispersal on male survival and reproductive success. If early dispersal improves male survival, then early dispersers should be more likely to survive to reproductive maturity, and should be over-represented in all age classes. If early dispersers accrue reproductive benefits, they should be more likely to be observed mating than late dispersers, and they should be able to mate with greater numbers of different mating partners than males that delay emigration.

METHODS

Study population

This study was conducted in a 20-hectare meadow located in the Sierra Nevada Mountains near Tioga Pass in Mono County, CA. Sherman and Morton (1984) describe the study site in detail. Between May and September from 1993 to 2003, individual squirrels on the study meadow were trapped at regular intervals using Tomahawk live-traps baited with peanut butter and released at their original capture sites. Each squirrel was weight to the nearest 1 g using spring balances, and the capture location was recorded. An individual's reproductive condition was evaluated, and males were considered reproductively mature if they showed descended testes during the mating period at the onset of the active season. Males of this species reach sexual maturity at age 2. At first capture, individuals were marked with metal ear tags and hair dye to facilitate visual identification (Sherman 1976). The location of each adult female's nest burrow was identified by observing the female's activity daily throughout the summer. Juveniles were first trapped within 4 days of their initial emergence above ground at weaning, during which time they could be unambiguously assigned to a mother (Sherman, 1976).

The dispersal age of each male was established using methods developed by (Holekamp, 1983; Holekamp, 1984a). Marked litters were observed at dawn and dusk to determine if they were still sleeping in their natal areas. Based on the maximum radius of 80 m of a maternal territory, a male's natal area was defined as a circle of 160 m in diameter centered on the male's natal burrow (Holekamp 1983). Males were considered absent from their natal area if they were not seen exiting their natal burrow at dawn or entering the burrow at dusk. If a male did not spend the night in his natal burrow, extensive trapping and visual observations were performed on the study meadow and environs in an attempt to relocate him. Males were considered to have dispersed during their juvenile summer if they were not observed in their natal areas late in the summer but were subsequently relocated elsewhere. These males were considered early dispersers whereas males that over-wintered in their natal area were considered late dispersers. We were unable to assign dispersal age to some males since they had disappeared from their natal site, and we were unable to relocate them on our study site or the surrounding areas. However, some of these males disappeared before they had reached eight weeks of age, while others disappeared after eight weeks of age. Since previous work by Nunes et al. (1998) has shown that only a small proportion of males disperse at seven weeks of age, I made the assumption that males of the first group had died while still at their natal site while males that disappeared after eight weeks of age were early dispersers that died during dispersal. As a result, males that disappeared after 8 weeks of age could have died at their natal site, died after dispersing or dispersed and not been recovered, it is possible that I slightly overestimated the juvenile mortality of early dispersers using this criteria.

Fitness parameters & data analysis

Trapping data collected between 1993 and 2003 were used to determine survivorship of early- and late-dispersing males. Data for survivorship analyses came from the five cohorts (1993 - 1997) for which there were complete records of survivorship as all males from these cohorts had died by 2003. For each age class, a male was considered to be alive if he was captured at least once during a given year and was otherwise considered to have died. Horizontal life tables were constructed separately for early- and late-dispersing males following the methods of Sherman and Morton (1984). First, the number of individuals that were alive at age x (n_x) and the number of individuals that did not survive to the next age (disappearance, d_x) were tabulated. Survival rate (l_x), disappearance rate (q_x) and future life expectancy (e_x) were calculated following Deevey (1947) and Ricklefs (2000). The Cox's F test was used to compare age-specific survivorship (l_x) between early- and late-dispersing males. Chi-squared analyses were used to assess whether early dispersers were more likely to survive to age one (juvenile survival) or to reproductive maturity (survival to age two) than were late dispersers. These analyses were based on the total number of males in each dispersal age group and the number of individuals that were still alive as one- or two-year olds, respectively.

In 1998, 6 observers monitored the study area for matings throughout the mating period (June 4 – 25) to assess differences in male mating success between early and late dispersers. Critical incident sampling and focal animal observations (Altmann, 1974) of adult males and females were used to monitor male mating behavior. During the mating season, critical incident sampling was conducted throughout the species' daily activity period (0730 to 1930), totaling 264 daytime hours. During this time, we also conducted 71 h of focal animal observations. When copulations were observed, the date, time, location, and identity of mating partners were recorded. During each active season, female *S. beldingi* are in estrus on only one day, for 3-4 h, and remain in a specific area of the study meadow throughout this period (Sherman, 1976; Sherman, 1977). Female estrus behavior could therefore be used to determine if a male had mated with the same or different female in three cases in which we were unable to determine the identity of a female mating partner. For example, if a male was observed mating with an unidentified female during the morning hours and a known female the following evening, we could be certain that these matings involved two different females. Using this method, we were able to determine that the identity of a male's unknown mate must have differed from that of his previous mating partner(s) in all three cases. Male and female *S. beldingi* may mate multiple times with the same mating partner (Sherman, 1976). I therefore chose to use "number of different mating partners" rather than "number of copulations" as our measure of male mating success. Dispersal ages were assigned to adult males based on previous trapping and observation records. Body mass is an important determinant of male mating success in Belding's ground squirrels (Sherman, 1976). As a result, differences in male mating success may be a consequence of differences in body mass rather than dispersal age per se. To account for this possibility, I compared the body mass of early- and late dispersers taken within ± 4 days of the middle of the mating season (June 14th).

Fisher's exact test was used to determine whether the probability of being observed mating differed between adult males in the two dispersal age groups. This comparison was based on the number of males from each dispersal age group observed mating, relative to their representation in the overall population of males trapped during the 1998 mating season. A chi-square test was used to assess whether the number of different mates acquired by males of known dispersal age varied in proportion to the number of males that mated in each dispersal class. Since data were not normally distributed (Lilliefors test, $p < 0.01$), a Mann-Whitney U test was used to compare the mean number of different mates acquired by males in each dispersal age group. T-tests were used to compare the mid-mating season body mass of early- and late dispersers. The statistical package STATISTICA 6.1 (StatSoft Inc.) was used for all data analyses. Two-tailed *p*-values are reported for statistical tests, and results were considered significant if $p < 0.05$. Means are reported ± *SE*.

RESULTS

Survivorship

Between 1993 – 1997, 433 juvenile males from 153 different litters were trapped and tagged (Fig. 1). Dispersal ages could be unambiguously assigned to 239 males, including 149 early and 90 late dispersers. For the remaining 194 males, 113 of them disappeared before they had reached age week 8 while 81 males disappeared after age week 8. We added the number of individuals that had disappeared after age week 8 ($n = 81$) to the number of males ($n = 149$) we were able to unambiguously categorize as early dispersers. Data from these males ($n = 230$) and from late dispersers ($n = 90$) were used to construct life tables for males in each dispersal age group (table 1). Age-specific survivorship (l_x) varied significantly between early and late dispersers (Fig. 2; $F_{460, 180} = 1.57$, $p < 0.000$). Early dispersers were significantly less likely to survive to age one than late dispersers (Fig. 3; $\chi^2 = 42.22$, $df = 1$, $p < 0.000$). However, the probability of surviving to reproductive maturity (age two) did not differ significantly between dispersal age groups ($\chi^2 = 0.74$, $df = 1$, $p = 0.390$). Survivorship analyses including only the subset of early dispersers with unambiguous dispersal age ($n = 149$) produced similar results, which are not reported here.

Mating success

During the 1998 mating season, 34 different adult males were trapped. Dispersal ages were known for 16 of these 34 males since some males had immigrated into the meadow from outside the study area as yearlings (age one; $n = 1$) or as adults ($\geq$ age two, $n = 16$). Of the 16 males with known dispersal ages (8 early and 8 late dispersers), 11 individuals (6 early and 5 late disperser) mated with a total of 22 different females (early dispersers mated with 16 females; late dispersers mated with 6 females). Dispersal age did not influence the likelihood of observing a male mating (Fisher's exact test, $p = 1.00$). Overall, however, the observed and expected number of female mating partners differed significantly between early and late disperses (Fig. 4; $\chi^2 = 6.60$, $df = 1$, $p < 0.010$). Furthermore, early dispersers mated on average with a greater number of different females than did late dispersers (Fig. 5; $Z = 2.02$, $p = 0.044$). Early- and late dispersers were similar in body mass when considering all males of known dispersal age (early dispersers: mean = 231 ± 12.01 g, late dispersers: mean = 229 ± 12.69 g; $t_{1,14} = 0.11$, $p = 0.911$) or only males that were observed mating (early dispersers: mean = 239.00 ± 14.47 g, late dispersers: mean = 232.40 ± 20.27 g; $t_{1,9} = 0.272$, $p = 0.792$). These results suggest that differences in mating success between early and late dispersers are not merely an artifact of male body mass.

DISCUSSION

My results suggest that early dispersal in Belding's ground squirrels is correlated with an increase in male fitness. Early dispersers acquired more, and late dispersers acquired fewer, mates than expected. Furthermore, early dispersers mated on average with a greater number of different females than did late dispersers. Anecdotal evidence suggests that dispersal age also influences mating behavior in the black-tailed prairie dog, *Cynomys ludovicianus* (Garrett and Franklin, 1988). In this species, males most frequently emigrate in the spring of their yearling active season, and males become reproductively mature as two-year olds. Yet, a few unusually large individuals may emigrate when they are very young, prior to their first winter. These large males also reach sexual maturity at age one and are able to acquire mates at this age. Although a rare event, this observation suggests that male prairie dogs that are able to disperse at an early age may also enjoy a reproductive advantage.

However, male mating success may not necessarily provide an accurate measure of male reproductive success since in many ground-dwelling sciurids, including *S. beldingi*, females mate with multiple mates and produce mixed paternity litters (reviewed by Travis et al., 1996; Lacey et al., 1997). In ground-dwelling sciurids, the frequency of multiple paternity ranges from 3 % in *C. ludovicianus* (Hoogland and Foltz, 1982) to 88.9 % in the California ground squirrel, *Spermophilus beecheyi* (Boellstorff et al., 1994). In *S. beldingi*, multiple paternity estimates range from 32 to 66 %, and similar to the Arctic (*Spermophilus parryii*) and thirteen-lined ground squirrel (*Spermophilus* *tridecemlineatus*), a female's first mating partner sires the greatest proportion of offspring in a female's litter (Foltz and Schwagmeyer, 1989; Lacey et al., 1997; Sherman, 1989). Unfortunately, our data were insufficient to determine the mating sequences of males. However based on his data and extensive behavioral observations, Sherman (1989) proposed that the evolutionary stable mating strategy for a male *S. beldingi* should involve mating with as many females as possible. If a male's mating success reflects the number of pups he sires, early dispersers should therefore sire a greater number of pups than late dispersers. Clearly, future genetic analysis of paternity comparing males of different dispersal ages will be helpful to confirm the differential mating success of early and late dispersers I observed in this study.

The influence of dispersal age on male mating success has also been documented in some species of primates. For example, in both savannah baboons (*Papio cynophalus)* and long-tailed macaques (*Macaca fascularis*), the reproductive potential of males is highest when they are physically and socially at their prime, but the timing of dispersal relative to this prime differs between the species, as does the relative size and age at which males disperse. Male *P. cynophalus* emigrate shortly after reaching adult body size, and tend to rise quickly to the top of the dominance hierarchy in the new troop (Alberts and Altmann, 1995). By contrast, male *M. fascularis* disperse when they are not yet fully grown, and enter the new troop at the bottom of the dominance hierarchy (Noordwijk and Schaik, 2001; van Noordwijk and van Schaik, 1985). Occasionally, male *M. fascularis* attempt to immigrate into a new troop when they are fully grown, but these males are almost always rebuffed by the local alpha male. This suggests that factors other than a male's physical condition influence the immigration success of male *M. fascularis*. Van Noordwijk and Schaik (2001) proposed that prolonged residence in the new troop allows a young male to monitor and judge the stability of the dominance hierarchy and use this knowledge to determine when the alpha male is most vulnerable to rank challenges. Hence, physical prowess is critical for the outcome of rank challenges in *P. cynophalus*, whereas *M. fascularis* males must gather and apply new social knowledge in order to maximize their take-over prospects.

In *S. beldingi*, male-male competition for mates is intense, and a male's ability to win fights influences his mating success (Sherman, 1976). Thus, enhanced competitive abilities reflected in greater fighting success of early than late dispersers may have been responsible for the enhanced mating success of early dispersers in 1998. Although *S. beldingi* males do not defend exclusive territories, early dispersers may have also been more effective than late dispersers at excluding other males from receptive females (Lacey and Wieczorek, 2001). Receptive female *S. beldingi* appear to stimulate male-male competition, observe male fights, and then solicit some males while rejecting others, suggesting that females in this species actively choose male mating partners (Sherman 1976). Consequently, the differential mating success we observed might have been due to females preferentially mating with early dispersers. Further work will be necessary to assess the relative contribution of male competitive ability and female mate choice in determining the differential mating success between males of the two dispersal groups.

Early dispersers were significantly less likely to survive their first year of life than late dispersers, suggesting a tradeoff between early dispersal and survival for male *S. beldingi*. Exceptionally high losses of juveniles relative to adults have been observed in many ground-dwelling sciurids and have been attributed to greater vulnerability of young squirrels to predation and over-winter mortality (yellow-bellied marmot, *Marmota flaviventris,* Armitage and Downhower, 1974; Richardson's ground squirrel, *S. richardsonii*, Michener and Michener, 1971; *S. parryii*, Byrom and Krebs, 1999). In addition, young dispersers may be especially vulnerable to these mortality factors since extensive locomotor behavior can increase predation risk (Metzgar, 1967) and reduce or limit the amount of energy stores young animals have available for hibernation (Buck and Barnes, 1999a; Nunes et al., 1999). In *S. parryii*, juveniles are exposed to high predation rates during dispersal but their survival rate remains constant after settlement (Byrom and Krebs, 1999). Our data suggest that about 44% of early dispersers (81 of 183 juvenile losses) died during transit indicating that predation risk may be an important source of mortality for young dispersers in *S. beldingi*. However, a significant number of juvenile losses occurred post-settlement suggesting that other factors, such as over-wintering mortality, are responsible for juvenile losses as well.

Available energy stores are crucial for over-winter survival, and individuals with low body mass and small stores of body fat should therefore experience high mortality rates during hibernation (Lenihan and Van Vuren, 1996). The amount of energy individuals can store is directly proportional to their body size. Higher losses of early dispersers may thus be due to the smaller size and lower energy stores of early than late dispersers prior to their entry into hibernation. Placement and other characteristics of hibernacula might also influence over-winter survival (Buck and Barnes, 1999b). Young dispersers may not select appropriate hibernation sites or may not have sufficient time or energy available to build or modify a hibernaculum that provides sufficient protection from low temperatures during the hibernation period (Arnold, 1993).

The survival costs associated with early dispersal suggest a tradeoff that may be responsible for the maintenance of the dispersal age dichotomy in *S. beldingi*. In this species, circannual timing mechanisms tightly regulate dispersal behavior of males and inhibit dispersal if individuals fail to reach a specific body mass/body fat threshold early enough in the season to maximize their chances of surviving both dispersal and hibernation (Nunes et al., 1998). This is especially evident in years when a prolonged snow cover significantly shortens the species' active season and most males born during such short seasons disperse late (Nunes et al., 1998). The extent of growth males are able to complete during their juvenile summer also appears to affect dispersal age among males of other ground-dwelling sciurids (Chapter four). In most marmot species, males are only able to acquire less than 50% of adult body mass by the end of their juvenile summer, and in these species males consistently delay dispersal until they are older (Blumstein and Armitage, 1999). In the Columbian (*S. columbianus*) and

Richardson's ground squirrels exceptionally small males disperse several months after most males emigrate (Festa-Bianchet and King, 1984; Michener and Michener, 1977; Wiggett and Boag, 1991). In these species, as in Belding's ground squirrels, the need for juveniles to accumulate sufficient energy stores to survive hibernation appears to constrain dispersal, suggesting that energetic constraints have played an important role in shaping dispersal age among many ground-dwelling sciurids.

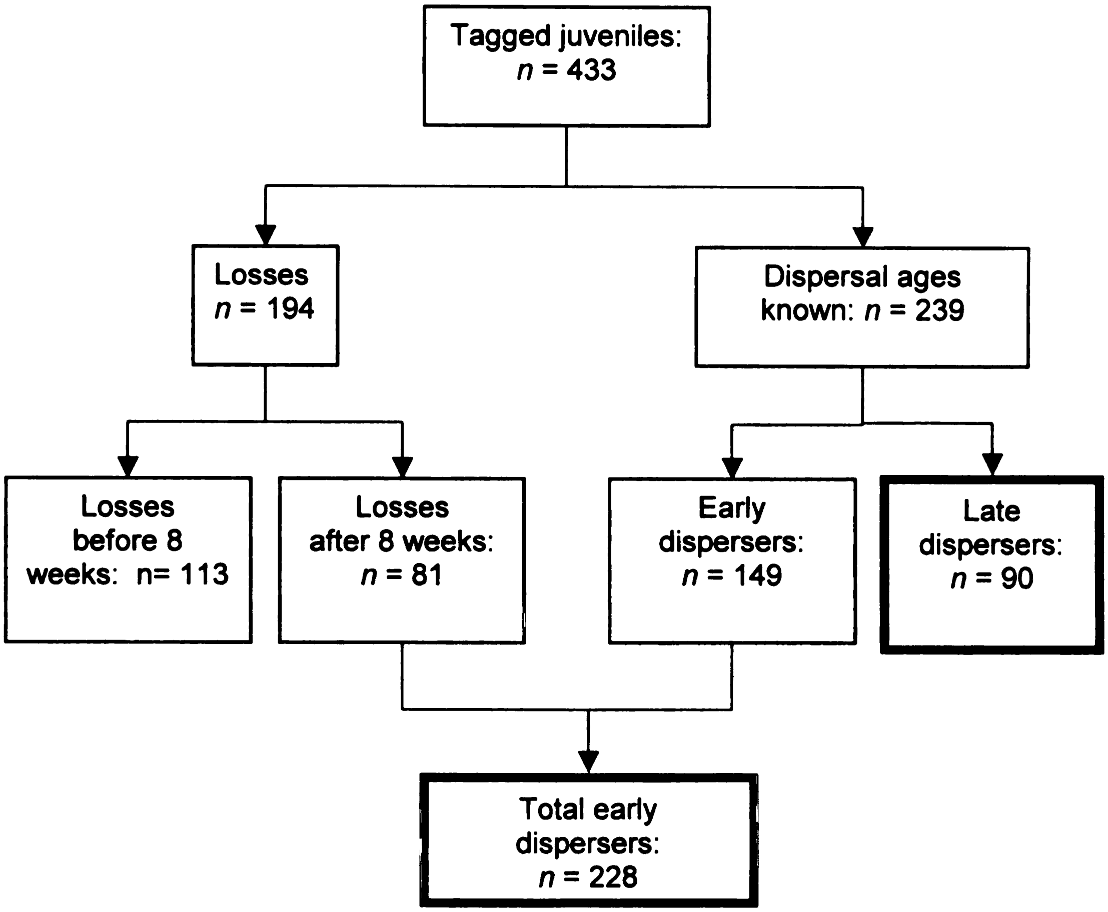

Figure 1. Summary of sample sizes obtained from monitoring male survival and dispersal behavior of 1993 – 1997 cohorts on Tioga pass meadow, CA. Out of 433 tagged juvenile males, I categorized 230 individuals as early dispersers and 90 individuals as late dispersers (see *Methods: Dispersal age assignment*).

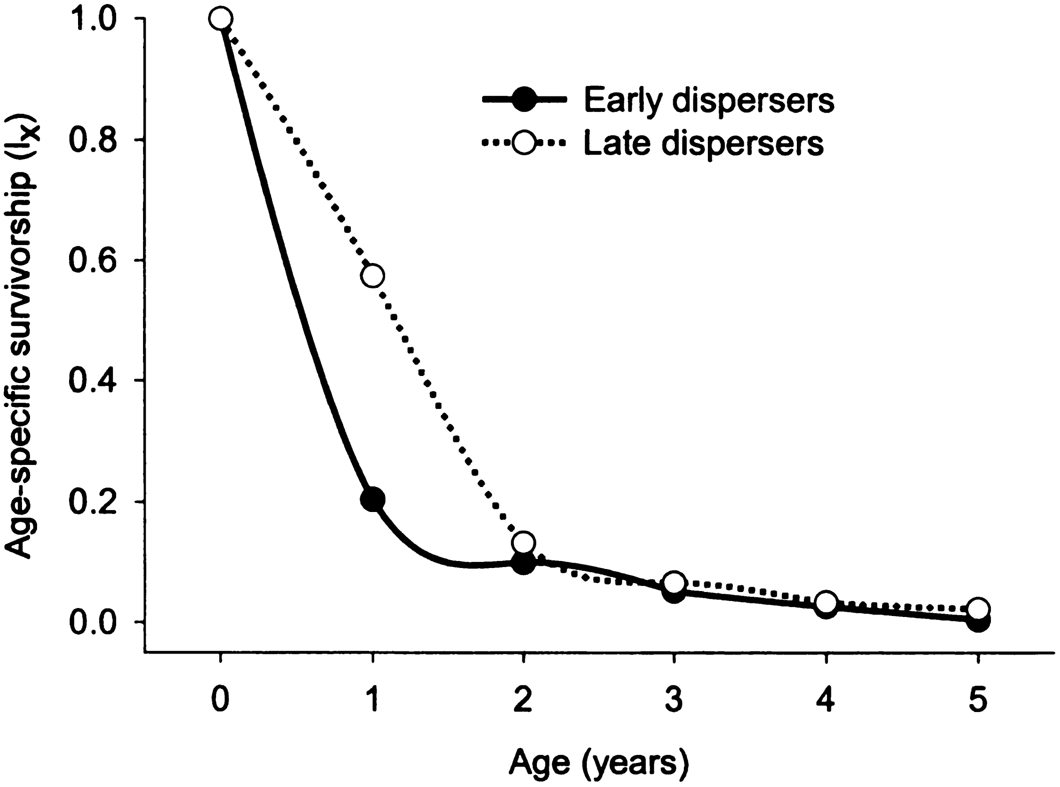

Figure 2. Age-specific survivorship of early- and late-dispersing males. Survivorship is based on 320 males, 230 early and 90 late dispersers, from cohorts born in 1993 - 1997.

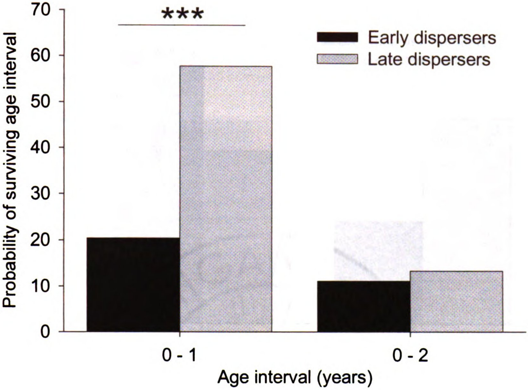

Figure 3. Percent of early and late dispersers surviving their first summer (to age one) and to sexual maturity (age two). Data are based on 320 males, 230 early and 90 late dispersers, from cohorts born in 1993 - 1997. Asterisks indicate significant differences between groups at $p < 0.001$.

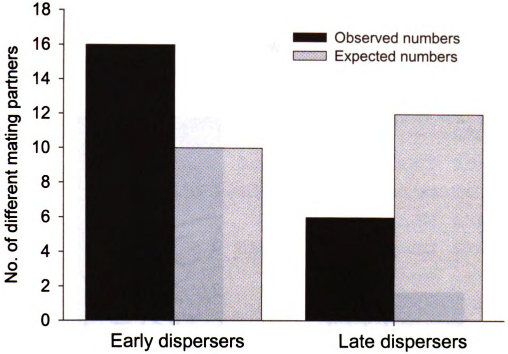

Figure 4. Observed and expected mating partners of early- and late-dispersing males. Expected values were calculated by assuming that early and late dispersers mated with females in direct proportion to the number of males in each dispersal age category observed mating.

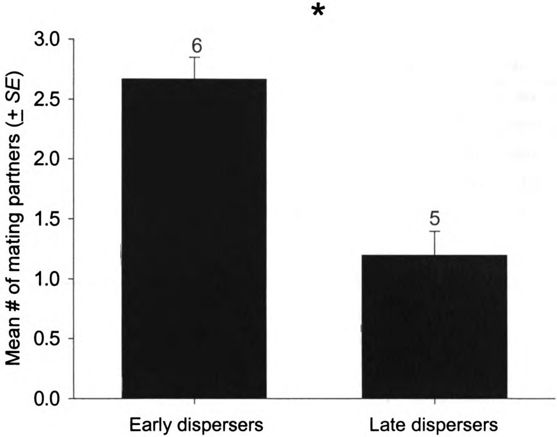

Figure 5. Mean number of mating partners (± *SE*) acquired by early and late dispersing males during the 1998 mating season. Asterisk indicates significant differences between groups at $p < 0.05$.

Table 1. Age-specific life table for early and late dispersing male *S. beldingi*, based on disappearance from the population of members of cohorts born in 1993 - 1997.

	Early dispersers					**Late dispersers**				
Age (years)	n_x	d_x	l_x	q_x	e_x	n_x	d_x	l_x	q_x	e_x
0	230	183	1	0.511	1.627	90	38	1	0.769	2.169
1	47	24	0.204	0.478	0.979	52	40	0.575	0.500	0.650
2	23	11	0.100	0.500	1.083	12	6	0.133	0.500	1
3	12	6	0.052	0.833	1	6	3	0.066	0.333	1
4	6	5	0.026	0.500	0.600	3	1	0.033	0.750	1
5	1	1	0.004	1	...	2	2	0.022	1	...
6	0	...	...	...	...	0	...	...	...	...

CHAPTER FOUR

GROWTH LIMITATIONS AND AVOIDANCE OF RESIDENT AGGRESSION INFLUENCE AGE AT DISPERSAL IN GROUND-DWELLING SCIURIDS

INTRODUCTION

Natal dispersal, the permanent departure of an individual from its birth site, is an important event in the life history of most mammals and birds (Greenwood, 1980; Lidicker, 1975). In natal dispersal, the disperser leaves behind the safety of a familiar social and physical environment and ventures into unfamiliar terrain in its search for a new home (Isbell and Van Vuren, 1996; Waser and Jones, 1983b). This can be costly since the increase in locomotor activity associated with this behavior can deplete a disperser's energy resources (Holekamp, 1986; Rood, 1987), and make the individual more vulnerable to predation (Metzgar, 1967). Compounding this effect, the threat of attack by hostile resident conspecifics may force a disperser to reduce foraging time in order to increase vigilant or defensive behavior, or prevent an individual from immigrating into a new site in suitable habitat (e.g., Garrett and Franklin, 1988). The prevalence of natal dispersal among birds and mammals suggests that dispersal costs are offset by significant fitness gains such as avoiding inbreeding and increasing reproductive opportunities (Dobson, 1982; Lehmann and Perrin, 2003; Moore and Ali, 1984; Pusey, 1987; Shields, 1982). Yet, the need to minimize dispersal costs relative to fitness gains theoretically should have played a crucial role in shaping the evolution of this behavior.

Evidence from a wide range of species suggests selection has favored evolution of behavior patterns that minimize the risks associated with dispersal. Frequently dispersers will use their birth site as a secure base from which they undertake extensive exploratory forays prior to dispersal (wolves, *Canis lupus*, Van Ballenberghe, 1983; Belding's ground squirrels, *Spermophilus beldingi,* Holekamp, 1986). In addition, dispersers may emigrate during periods when food is abundant, when vegetation provides cover from predators (black-tailed prairie dogs, *Cynomys ludovicianus,* Garrett and Franklin, 1988), or when safe travel routes are most likely to be available (beavers, *Castor canadensis*, Sun et al., 2000). Individuals may also disperse at an age when they are able to effectively counter aggression directed at them by local residents (savannah baboons, *Papio cynophalus,* Alberts and Altmann, 1995) or at an age when they are likely to confront low levels of aggression from local residents (Japanese macaques, *Macaca fuscata*; reviewed by Sprague, 1992).

In mammals, dispersal tends to be male-biased; males usually disperse at either higher rates or over longer distances than females (Greenwood, 1980; Lidicker, 1975). Males of many mammalian species emigrate before they have completed growth and maturation, but dispersal ages vary among species (Dobson, 1982) suggesting that selection may have shaped this behavior to occur at an age when an individual is best able to cope with the risks and challenges of dispersal. Ground-dwelling sciurid rodents show the dispersal patterns characteristic of most mammals, exhibit a range of dispersal ages, and, as a consequence, are an ideal group in which to examine the role of selective agents in shaping the evolution of dispersal age in mammals.

Ground-dwelling sciurid rodents includes the antelope squirrels (*Amospermophilus* spp.), ground squirrels (*Spermophilus* spp.), marmots (*Marmota* spp.), and prairie dogs (*Cynomys* spp.) and, with the exception of *Amospermophilus*, much is known about the life history of the members in this group (Murie and Michener, 1984). All species share a common life style in that they are all diurnal vegetarians, and most live in underground burrows (Nowak, 1999). Most species also hibernate during the winter or aestivate during the summer months, during which time they rely primarily on stored fat as an energy source. Females of most species produce only one litter each year. Mating occurs at the onset of the active season, followed by a 3-5 week gestation period. Litters emerge above ground towards the end of the lactation period, when adults begin fattening in preparation for dormancy. In most species, male dispersal occurs prior to first reproduction (see Blumstein and Armitage, 1998) for exceptions). Although males of each species predictably emigrate at a specific age, dispersal age varies significantly among sciurid species. That is, males of some species emigrate as juveniles, during the year in which they are born, whereas males of other species consistently tend to delay dispersal until they are 1, 2, or 3 years of age (reviewed by Holekamp, 1984a; Blumstein and Armitage, 1998; Holekamp, 1984a).

Ground-dwelling sciurids show also differences in a variety of life history, ecological, and social factors. For example, adult body mass varies greatly among ground-dwelling sciurids (reviewed by Armitage, 1981), ranging from 135 g (thirteen-lined ground squirrel, *S. tridecemlineatus*) to 5000 g (yellow bellied marmots, *M. flaviventris*). In addition, the duration of the active season varies among species from 4.5 months (Olympic marmot, *M. olympus)* to 9 months (round-tailed ground squirrel, *S. tereticaudus*), and one species, the black-tailed prairie dog (*C. ludovicianus)*, is active throughout the year. Ground-dwelling sciurids with short active seasons tend to live at high elevations or high latitudes, where winters are long and severe. Species with longer active seasons are found at lower elevations and in regions where climatic conditions are relatively mild. Evidence from several species suggests that growth of immature sciurids is limited by the duration of the active season and by adult body size because juveniles must balance the amount of energy they allocate towards somatic growth with the need to accumulate adequate fat stores to survive dormancy (Barash, 1973; Webb, 1981; Armitage, 1981; Zammuto and Millar, 1985; Van Vuren, 1990*;* Dobson, 1992; Arnold, 1993). Ground-dwelling sciurids occupy a variety of different habitats ranging from vast expanses of continuous grassy terrain (Columbian ground squirrel, *S. columbianus;* Arctic ground squirrel, *S. parryii*) to regions in which suitable habitat patches are small and separated by rocky outcroppings or mountains (*M. flaviventris,* Armitage, 1981). The social organization of ground-dwelling sciurids is also variable and ranges from solitary (groundhog, *M. monax*) to complex stable social groups (*M. olympus*, *C. ludovicianus;* reviewed by Michener, 1983). Depending on the social system, adult males, adult females, or adults of both sexes defend territories against intruding conspecifics during specific periods or throughout the active season. Overall, it seems reasonable to expect that variation in life history, ecology, and sociality have played important roles in shaping the evolution of dispersal age in ground-dwelling sciurids.

Three hypotheses have been put forward to explain the variation observed in the timing of natal dispersal among ground-dwelling sciurids. The growth limitation hypothesis posits that males delay dispersal until they have acquired sufficient energetic resources to support the demands of dispersal and hibernation (Armitage, 1981; Barash, 1974). This hypothesis predicts that the extent of growth males are able to complete during their first summer determines dispersal age. The risk avoidance hypothesis states that males delay emigration until they are older and better able to cope with the risks of dispersal, or until the costs of remaining at the natal site exceed the costs of dispersing (reviewed by (Arnold, 1993; Emlen, 1991). Travel over long distances and across unsuitable habitat increases mortality risk for dispersers (Arnold, 1993; Van Vuren, 1990; Webb, 1981). This hypothesis predicts that males should delay dispersal in species where dispersers have to travel long distances to locate suitable settlement sites. Lastly, the social resistance hypothesis suggests that aggression by local residents creates a significant barrier to potential immigrants, and dispersers that are unable to avoid or counter this aggression effectively may be forced into marginal habitat where an individual's prospects for survival and reproduction are significantly reduced (Armitage, 1999; Garrett and Franklin, 1988). Since older males should be better able to counter aggression by local residents, males from species in which immigrants are likely to be targets of aggression should disperse at an older age than males from species in which immigrants encounter little aggression.

The goal of this study was examine dispersal patterns of ground-dwelling sciurids to further investigate factors affecting the evolution of dispersal age among mammals. Specifically, I conducted a review of existing literature on ground-dwelling sciurids to identify field studies documenting ecology and natural history relevant to dispersal age. I combined these data with a phylogenetic hypothesis developed for ground-dwelling sciurids (Herron et al. 2004) to evaluate the growth limitation, risk avoidance and social resistance hypotheses.

METHODS

Data set

A thorough review of the ground dwelling sciurid literature was conducted. When possible, variables were recorded from the identical study and/or study populations to minimize variance in the data set due to differences in research methods and/or variation in behavior and ecology among populations.

1. <u>Dispersal age (wks).</u> Dispersal age was determined by calculating the number of weeks elapsing between the date pups were first observed above ground and the date when males were initially observed emigrating from their natal site. This measure was selected because number of days between parturition and the date on which pups first emerge above ground is unknown for many ground-dwelling sciurids. For *S. armatus, S. citellus,*

C. leucurus and *S. franklinii* authors reported males dispersed as juveniles but did not specify the exact age. I assigned dispersal ages to these four species assuming that males dispersed midway through their juvenile active season. This was a reasonable assumption considering that in most species where juvenile dispersal occurs males emigrate during the middle of the species' juvenile active phase (Byrom and Krebs, 1999; Holekamp, 1983; Olson and Horne, 1998).

2. Juvenile maturity index (MI_j). Growth juvenile males were able to complete during their first active season relative to the species' adult body size was calculated using the juvenile maturity index (MI_j) developed by (Barash, 1973). This index provides a measure of the total somatic growth occurring during the juvenile summer relative to a species' body size at maturity. MI_j was calculated by dividing the post-emergence body mass of yearling males by the minimum adult male body mass. Minimum adult body mass was determined using the early season body mass of adult males when reported, or the minimum body mass of adult males from the range of values provided (Armitage, 1981; Blumstein and Armitage, 1999).
3. Age at adult body mass (wks). Following previous investigators (Armitage, 1981; Barash, 1973), I used age at adult body mass as an indicator of how much time males require to complete growth and sexual maturation. I defined the age at which males reached adult body mass to be the year in which they had achieved minimum adult body mass by the onset of the mating season that year.

4. Effective dispersal distance. The effective dispersal distance for each species was calculated by dividing the mean dispersal distance of males by the mean home range diameter reported for the same species. This corrects for differences in home range size among species (Shields 1982). Mean dispersal distance is the mean straight-line distance (m) between a male's natal burrow and a male's settlement site after dispersal. Mean home range diameter was defined as the mean diameter (d) of the home range reported for individual females or social groups. When only the mean home range size (m^2) was reported, home range diameter was calculated as follows: $d = \sqrt{}\,(\text{Area} / \pi) * 2$.

5. Social agression score. A social aggression score was determined for each species based on levels of resident aggression during the dispersal period. Dispersal period was defined as the time between the first and last date males were observed emigrating from their natal area. To determine levels of resident aggression, we noted when aggression was reported during a species' active season, as well as the sex of the main aggressor(s). Presence of territory defense, wounding patterns, and aggressive interactions among conspecifics were used as indicators of high levels of resident aggression; these events were previously reported as good measures of resident aggression in ground-dwelling sciurids (e.g., Garrett and Franklin, 1988; Millesi et al., 1998; Sherman, 1976). A score of '1' was assigned if the dispersal period did not coincide with high levels of resident aggression. If adult female, adult male, or adult male and

female aggression was reported, a score of '2,"3,' or '4' was assigned, respectively. Male aggression was scored higher than female aggression, since male aggression is more intense and can result in serious injury or death (Garrett and Franklin, 1988; Huber et al., 2002; Sherman, 1976).

Comparative methods

Closely related species may share common traits due to shared ancestry rather than independent evolutionary events (reviewed in Martins, 2000). As a result, comparative data are not statistically independent and violate one of the basic assumptions of statistical tests (Felsenstein, 1985; Purvis and Rambaut, 1995). To remove the issue of non-independence in data sets, comparative methods have been developed which examine relationships among pairs of traits using phylogenetic hypotheses to accounting for potential effects of shared evolutionary history. To assess the relationships among pairs of behavioral traits the independent contrast method of Felsenstein (1985) was implemented using the Comparative Analysis of Independent Contrasts (CAIC, version 2.6.9, Purvis and Rambaut, 1995). In CAIC, we selected the CRUNCH algorithm, which generates phylogenetic independent contrasts (PICs) for continuous traits.

PICs assume a fully re-solved and accurate phylogeny and branch lengths can be used as an estimate of expected variance in character evolution. I approximate the phylogenetic relationships of the species for which I were able to extract data from the literature using Herron et al.'s (Herron et al., 2004) hypothesis (Fig. 3 in Herron et al., 2004) of phylogenetic relationships within the sciurid family of rodents. Herron et al.'s (2004) hypothesis was generated using Bayesian phylogenetic analysis based on mitochondrial cytochrome *b* sequences from 114 species in 21 genera, and currently provides the best approximation of the evolutionary relationships among species of ground-dwelling sciurids. I constructed a modified phylogenetic hypothesis (Fig. 1) including the 22 species from our study by creating a pruned tree constructed in McClade 4.06 (Maddison and Maddison, 2000). To generate branch lengths, I linked this tree with a matching data set of mitochondrial cytochrome *b* gene sequences from Herron et al. (2004; see appendix for GenBank accession numbers). Branch lengths were based on differences in base pair substitutions of the cytochrome *b* sequences. Branch lengths were generated in PAUP 4.0.b10 (Swofford, 2002) with our optimality criterion set to minimum evolution distance using maximum likelihood parameters from the GTR + G + I model of Herron et al. (2004) and limited to nonnegative branch length values (Fig. 1).

Following other comparative studies (Hagman and Forsman, 2003; Mermoz and Ornelas, 2004; Summers and Clough, 2001), I examined the relationships among pairs of related traits under three different models of character evolution: the Brownian motion (BM) model, the punctuated equilibrium (PE) model, and the star phylogeny model. The first two methods could be utilized in CAIC. The BM model states that character changes occur along branches between speciation events and variations among species are contingent upon when species diverged from their common ancestor (Diaz-Uriate and Garland, 1996; Felsenstein, 1985). For this model, PICs were calculated using branch lengths as a proxy for time since evolutionary divergence. Since CAIC does not accept branch lengths less than 2 units, we multiplied all branch lengths by 10,000 and added 2 units to all branch lengths (Purvis and Rambault, 1995). The PE model of character evolution states that changes in characters are associated with speciation events and, as a result, all character state changes occur at the nodes of the phylogeny. For this model, PICs were calculated by setting branch lengths to unity (Diaz-Uriarte and Garland, 1996). Lastly, the star phylogeny assumes that taxa diverged rapidly from a common ancestor, and the resulting phylogeny can be viewed as a star since all species radiate from a single point and all branch lengths are equal (Martins, 2000). As a consequence, species can be treated as independent units, and raw species' data were used to examine the relationship among traits of interest.

Regression analyses

PICs generated under the BM and PE model and the raw data were used to conduct regression analyses to address the predictions of the growth limitation, risk avoidance, and social resistance hypotheses (Table 1). In these analyses, I used dispersal age as the dependent variable and variables 2-5 as the independent variables:

1) To test the growth limitation hypothesis, I examined the relationship between dispersal age and two growth parameters, juvenile maturity index and age at adult body mass. If growth limitations influence dispersal age, little total

growth during a male's first summer should lead to a delay in dispersal resulting in a negative relationship between dispersal age and juvenile maturity index. In species' in which males complete growth early in life, males should be able to disperse at a young age, resulting in a positive relationship between dispersal age and age at adult body mass.

2) To test the risk avoidance hypothesis, I examined the relationship between dispersal age and effective dispersal distance. I expected to observe a positive relationship between these two variables since dispersal should be delayed in species in which males have to travel great distance before they are able to settle in a new place.

3) Lastly, I examine the social resistance hypothesis to assess the relationship between dispersal age and social aggression score. I expected to observe a positive relationship between these two variables since males should delay dispersal in species where resident aggression is high during the dispersal period and until they are older and better able to counter this aggression.

To examine these hypotheses simple and multiple regression analyses were performed using independent contrasts generated in CAIC (BM and PE model) and raw data (star phylogeny model). Simple linear regression analyses for contrast data were performed in CAIC; simple linear regression analyses for raw data and multiple regression analyses for contrast and raw data were performed in STATISTICA for windows version 6.1 (StatSoft). For independent contrast data, regression analyses were forced through the origin as required for PICs (Garland et al., 1992). Prior to generating contrasts or analysis, data were log-transformed (MI_j, age at adult body mass, and effective dispersal distance) or square-root transformed (social aggression score) to best meet statistical assumptions associated with regression analyses. Data were inspected for significant outliers (studentized residuals greater than 3; Jones and Purvis, 1997), and homogeneity of variance with no significant violations. I did not include effective dispersal distance in the multiple regression analyses since inclusion of this variable in the model would have substantially reduced sample sizes. Sample sizes refer to the number of species used in regression analyses; these vary due to missing values of some variables for some species. Two-tailed P - values, and results were considered significant if $P < 0.05$. Means are reported ± standard error.

RESULTS

I were able to determine dispersal ages of males for a total of 22 ground-dwelling sciurids; including 6 of the 14 extant marmot species (*Marmota* spp.), 3 of the 5 extant prairie dog species (*Cynomys* spp.), and 13 of the 38 extant ground squirrel species (*Spermophilus spp.*; Appendix). Dispersal ages ranged from 3 to 152 wks (mean = 33.8 ± 10.14 wks). I was able to calculate juvenile maturity indices for 20 species, which ranged from 0.37 to 1 (mean = 0.74 ± 0.052). Age at adult body mass varied from 35 to 146 wks (mean = 90.55, ± 7.82 wks, $n = 22$), and effective dispersal distances ranged from 0.45 to 25.8 home range diameters (mean = 6.16, ± 2.39, $n = 13$). Dispersal period did not coincide with resident aggression in 54 % ($n = 12$; aggression score one) of species, co-occurred with adult female aggression in 5 % (*n* = 1; aggression score two), adult male aggression in 18 % (*n* = 4; aggression score three), and adult male and female aggression in 23 % (*n* = 5; aggression score four) of species.

Results of the bivariate regression analyses under the three evolutionary models were summarized in Table 2. Contrasts were adequately standardized except for effective dispersal distance in the PE model where I observed a violation of the evolutionary assumption that standardized contrasts are independent of the estimated value of the character for the node at which the contrast was taken. As predicted by the growth limitation hypothesis, the amount of growth relative to their adult body mass males were able to complete during their juvenile summer (MI_j), showed a significant negative effect on the age at which males dispersed under all three evolutionary models. I observed a significant positive relationship between age at adult body mass and dispersal age under the star phylogeny, but not under the PE and BM evolutionary models. The relationship between effective dispersal distance and dispersal age was significant under the PE model, marginally significant under the star phylogeny, and non-significant under the BM evolutionary model providing inconsistent support for the risk avoidance hypothesis. I consistently observed the expected positive relationship between a species' social aggression score and dispersal age under all three evolutionary models, supporting the prediction of the social resistance hypothesis.

The results of the multiple regression analyses were consistent with those from bivariate regression analyses (Table 3). Across all three models, MI_j and social aggression scores significantly predicted dispersal age even after controlling for other variables in the model. Greater *ß* coefficients for MI_j than social aggression scores in these analyses indicate that MI_j contributes to a greater extent to the observed variation in dispersal age.

In summary, our results provide compelling evidence that early growth patterns and level of social resistance males encounter during the dispersal process were influential in shaping dispersal age in ground-dwelling sciurids. The relationship between effective dispersal distance and dispersal age were inconsistent under alternative evolutionary models and evolutionary assumptions of contrasts were violated under the PE model, making it difficult to evaluate the risk avoidance hypothesis. Further work with larger sample sizes and different measures of dispersal risk will be necessary to re-examine this hypothesis.

DISCUSSION

Our study provided does not allow us to reject the risk avoidance hypothesis, but provides compelling support for the growth limitation and social resistance hypothesis. No consistent relationship between a species' effective dispersal distance and dispersal age was detected. This result was unexpected since Byrom and Krebs (1999) documented an increase in mortality risk associated with greater dispersal distances in the Arctic ground squirrel, *S. parryii*. My measure of dispersal risk may have been too crude or have failed to encompass enough of the risks young males are exposed to during transit. Habitat patchiness, availability of refugia, habitat familiarity, and duration of transit may contribute significantly to risks males are exposed to during transit. Also, dispersal events reported in the literature are often biased towards short distance dispersal (Koenig et al., 1996) and dispersal distance is often measured as a straight line while a disperser's transit route rarely follows a direct pattern (Boydston et al., in press; Wiggett et al., 1989). In addition, my results may be due to insufficient sample sizes, making it difficult to detect a significant relationship between the variables. More work will be necessary before I can rule out the possibility that risk aversion has shaped survival of males and consequently the evolution of dispersal age in ground-dwelling sciurids and other mammals.

In support of the growth limitation hypothesis, a significant negative relationship between juvenile male growth and dispersal age was observed. This is consistent with the intraspecific variation in dispersal ages of males reported for several ground-dwelling sciurids. For example, in the Belding's (*S. beldingi*), Columbian, and Richardson's ground squirrel (*S. richardsonii)* exceptionally small males disperse several months after most males emigrate (Festa-Bianchet and King, 1984; Holekamp, 1986; Michener and Michener, 1977; Wiggett and Boag, 1991). In the black-tailed prairie dog (*C. ludovicianus*), unusually large males disperse several months before their same-aged, smaller counterparts (Garrett and Franklin, 1988). Body mass and body fat is the most important predictor of dispersal age in Belding's ground squirrels, and males of this species only emigrate as juveniles if they have reached a specific lean body mass/body fat ratio early in the species' active season (Nunes et al., 1998). Overall, results of interspecific studies are consistent with our findings implying that energy availability determines optimum dispersal age for survival and reproduction.

I observed a positive relationship between a species' dispersal age and social aggression score in support of the social resistance hypothesis. Immigrant males rarely encounter high levels of aggression in species in which males emigrate when they are only a few weeks old. At this age, males are still relatively small and immature, do not commit infanticide and, as a consequence, do not pose a threat to adult male or female residents. Furthermore, these males disperse after reproductive activities have ceased and adults are fattening for hibernation. Over-winter survival in ground-dwelling sciurids is critically dependent on the amount of energy stores individuals are able to acquire prior to hibernation (Lenihan and Van Vuren, 1996). Therefore adults are less likely to fend off potential immigrants while fattening. Dispersal at an early age does not always preclude young males from encountering aggression by local residents. Hibernacula are scarce in *S. parryii,* and adult male and female residents aggressively defend their hibernacula toward the end of their active season from other conspecifics, including juvenile immigrants (Carl, 1971). Evolution of dispersal at a very young age allows males to avoid resident aggression and increase survival in many but not all of the ground-dwelling sciurids included in this study.

Delayed dispersal may be adaptive when temporal avoidance of resident aggression is not possible because adults of one or both sexes defend territories throughout a species' active season. This is the case in most prairie dog (*C.*

ludovicianus; *C. gunnisoni*) and marmot species (e.g., *M. flaviventris*; hoary marmot, *M. caligata*; golden marmot, *M. caudata aurea*; *M. marmota*; Olympic marmot, *M. olympus*) in which the resident male or all members of a social group aggressively defend a common territory throughout the species' active season (Armitage and Downhower, 1974; Barash, 1973; Blumstein and Arnold, 1998; Garrett and Franklin, 1988; Hoogland, 1999; Michener, 1979a; Michener, 1979b). In many of these species a male's immigration success depends on his ability to displace a local male or to subsist in low quality areas until a habitat opening becomes available upon the emigration or death of a local resident male (*M. flaviventris,* Armitage and Downhower, 1974; *M. marmota,* Arnold, 1990). It is thus not surprising that males of these species generally disperse after they are relatively large and therefore presumably better able to counter resident aggression (Armitage 1981, 1999; Blumstein and Armitage, 1998) facilitating immigration.

The patterns I detected illustrate the importance of a species' developmental and social attributes in life history evolution. An important assumption of all three hypotheses examined in this study is that males are able to modulate their dispersal activity to maximize their probability of successful dispersal and immigration. Yet, males may not be able to do so if local residents evict young males from their natal site. In case of ground-dwelling sciurids, I can be confident that males of most species are not forced out of their natal areas since a considerable body of evidence has been gathered to reject this hypothesis (reviewed in Holekamp, 1984a). Although aggression is known not to

affect emigration in sciurids it apparently does affect immigration. However, future studies involving other species will need to examine this hypothesis before assessing the role of other selection pressures on shaping dispersal behavior. The possible influence of social resistance on dispersal age is intriguing, and I hope that future studies will examine the role of resident aggression in shaping dispersal and immigration patterns.

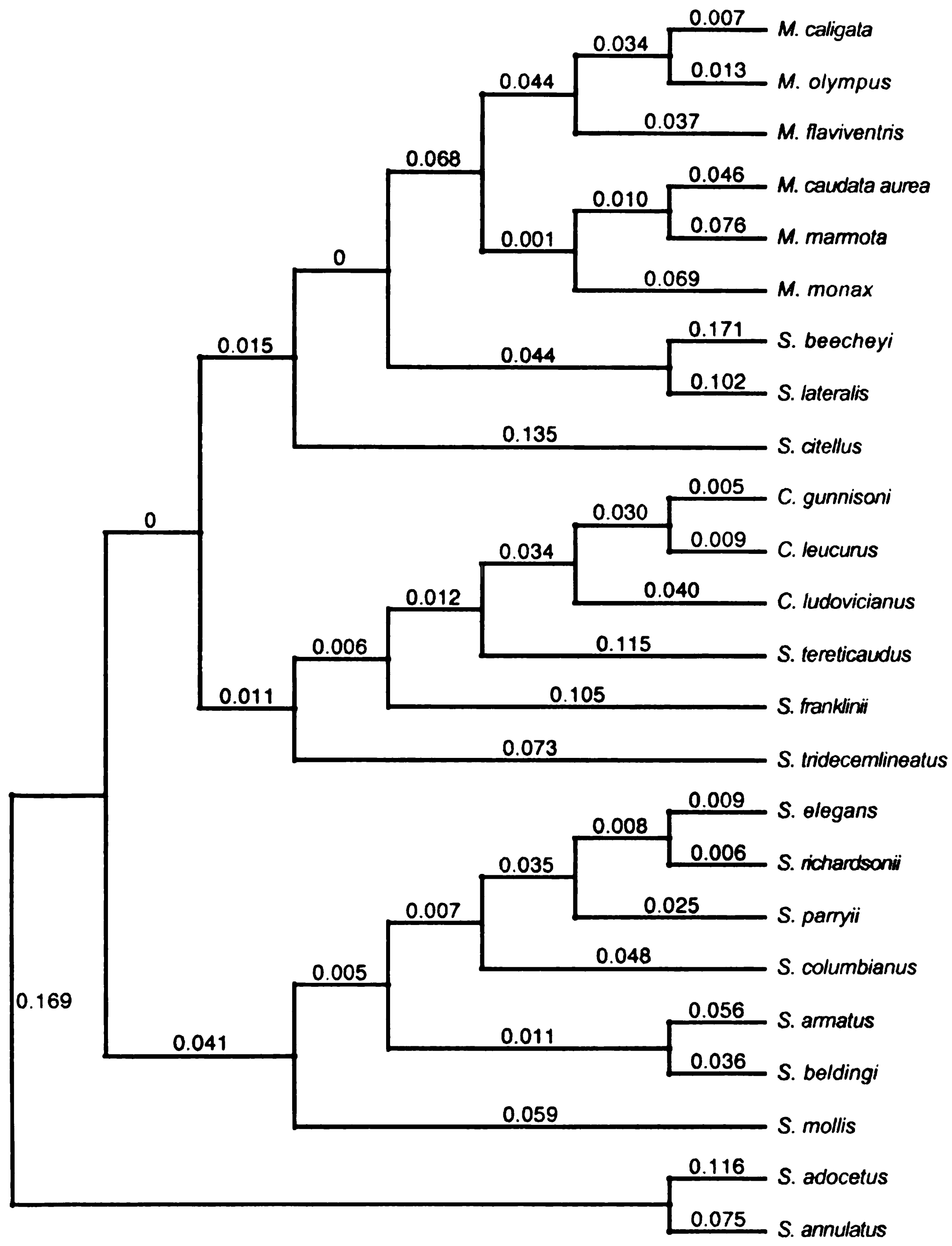

Figure 1: Phylogenetic tree of 22 ground-dwelling sciurid species used in the current study for comparative analyses. Numbers above branches indicate branch lengths, which were used as expected units of evolutionary change between speciation events for the Brownian motion model of character evolution.

Table 1. Proposed direction of relationship between predictor variables and dispersal age based on three different hypotheses.

Hypothesis	Predictor variable	Proposed direction of relationship
Growth limitation	Juvenile maturity index (MI_j)	-
	Age at adult body mass	+
Risk avoidance	Effective dispersal distance	+
Social aggression	Social aggression score	+

Table 2. Results of simple bivariate regression analyses of factors proposed to influence dispersal age in ground-dwelling sciurids

Brownian motion model

Term in model	*N*	*b*	*R*	Test statistics
Juvenile maturity index (MI_j)	20	-2.73	0.36	$F_{1,19}$=10.30 P=0.005
Age at adult body mass	22	0.24	0.02	$F_{1,21}$=0.54, P=0.470
Effective dispersal distance	13	0.32	0.17	$F_{1,12}$=2.21, P=0.165
Social aggression score	22	0.46	0.23	$F_{1,21}$=5.95, P=0.024

Punctuated equilibrium model

Term in model	*N*	*b*	*R*	Test statistics
Juvenile maturity index (MI_j)	20	-3.77	0.59	$F_{1,19}$=25.96, P<0.001
Age at adult body mass	22	0.45	0.05	$F_{1,21}$=1.09, P=0.309
Effective dispersal distance	13	0.57	0.35	$F_{1,12}$=6.01, P=0.032
Social aggression score	22	0.58	0.27	$F_{1,21}$=7.28, P=0.013

Star phylogeny model

Term in model	*N*	*b*	*R*	Test statistics
Juvenile maturity index (MI_j)	20	-3.14	0.61	$F_{1,19}$=28.54, P<0.001
Age at adult body mass	22	1.02	0.21	$F_{1,21}$=5.28, P=0.030
Effective dispersal distance	13	0.69	0.29	$F_{1,12}$=4.49, P=0.058
Social aggression score	22	0.94	0.48	$F_{1,21}$=18.53,P<0.001

N, number of species used to generate regression lines; *b*, slope of regression line. Results of binary linear regression analyses using independent contrasts that were generated using [a]varying branch lengths or [b]equal branch lengths, or [c]raw species data; [d]regression was forced through the origin.

Table 3. Results of multiple regression analyses of factors proposed to influence dispersal age in ground-dwelling sciurids.

Brownian motion model				
Term in model	*b*	*SE*	*ß*	Test statistics
Juvenile maturity index (MI$_j$)	-2.99	0.86	-0.66	$t_{1,16}$=-3.47 P=0.003
Age at adult body mass	-0.38	0.28	-0.26	$t_{1,16}$=-1.37, P=0.191
Social aggression score	0.43	0.17	0.44	$t_{1,16}$=2.59, P=0.020
Punctuated equilibrium model				
Term in model	*B*	*SE*	*ß*	Test statistics
Juvenile maturity index (MI$_j$)	-3.34	0.76	-0.68	$t_{1,16}$=-4.36, P<0.001
Age at adult body mass	-0.17	0.31	-0.09	$t_{1,16}$=-0.56, P=0.586
Social aggression score	0.39	0.19	0.32	$t_{1,16}$=2.06, P=0.056
Star phylogeny model				
Term in model	*b*	*SE*	*ß*	Test statistics
Juvenile maturity index (MI$_j$)	-2.16	0.59	-0.54	$t_{1,16}$=-3.69, P=0.001
Age at adult body mass	-0.15	0.30	-0.70	$t_{1,16}$=-0.50, P=0.622
Social aggression score	0.75	0.20	0.52	$t_{1,16}t$=3.81, P=0.002

b, slope of regression line; *SE,* standard error of regression slope; *ß*, beta coefficient of regression. Results of multiple regression analyses using independent contrasts that were generated using [a]varying branch lengths or [b]equal branch lengths, or [c]raw species data; [d]regression was forced through the origin.

CHAPTER FIVE

CONCLUSION

To understand why an animal exhibits a specific behavior it is necessary to examine the behavior from multiple perspectives. In 1961, Mayr proposed that it is important to examine causal explanations in biology from a proximate and ultimate level, where proximate factors influence the day-to-day life of an animal and ultimate factors determine how a trait is passed on across many generations and even across entire taxa. Expanding this framework, Tinbergen (1963) proposed that on a proximate level, it is necessary to observe the development of a behavior during the course of an individual's ontogeny and to elucidate the underlying physiological mechanisms that regulate a behavior. Furthermore, he suggested that on the ultimate level it is not only important to assess the fitness consequences of a behavior, but also to examine the behavior's evolutionary origin. An important implication of this framework is that there are at least four reasons why a specific behavior is observed. In order to fully understand a behavior it is also necessary to address all four levels of the Mayr - Tinbergen framework. In this chapter, I apply this general framework to address the question: "Why do most Belding's ground squirrel males disperse when they are relatively young?"

The Belding's ground squirrel, *Spermophilus beldingi*, is a small diurnal rodent. This species is active four months of the year, between May and August, and hibernates during the remaining eight months *S. beldingi's* short active season can be divided into two parts: breeding and post-breeding periods

(Sherman, 1976, Sherman, 1984). During the early part of the breeding period, mating occurs and males aggressively compete for access to mates. Shortly after mating, females establish territories, which they aggressively defend from other conspecifics throughout the breeding season (Nunes et al., 2000). Females give birth 25 days after having mated, and offspring remain in an underground burrow for the first 25 - 28 days of their life (Holekamp, 1983). The post-breeding period is marked by the emergence of juveniles from their natal burrow when youngsters become nutritionally independent from their mother. Adults begin fattening for hibernation shortly after juveniles emerge above ground.

As in most mammals, males are the predominant dispersing sex in *S. beldingi*, and 70 – 90 % of them leave their natal area as juveniles at 7 – 10 weeks of age, after having spent only 3 – 6 weeks above-ground (Holekamp, 1984b, Holekamp, 1986). The remaining 10 – 30 % of males delay dispersal until after their first hibernation as yearlings around 55 weeks of age. Since dispersal is a dangerous process (Byrom and Krebs, 1999; Garrett and Franklin, 1988; Larsen and Boutin, 1994) predominant juvenile dispersal by *S. beldingi* males seems to be a paradox since young males should be more vulnerable to the risks associated with dispersal than males that are older and more experienced. So, why do most *S. beldingi* males disperse as juveniles?

Kay Holekamp and her student Scott Nunes have shed light on this question by examining the proximate factors that regulate dispersal behavior in *S. beldingi*. Holekamp (1986)'s work illustrated that a male's dispersal age is contingent upon reaching a threshold body mass during a male's first active season. Males that reached this threshold during their first summer dispersed as juveniles, whereas males that were still relatively small at the end of their first active season delayed dispersal until after their first hibernation. Nunes expanded on Holekamp's work and revealed that males must not only reach a threshold body mass but, more specifically, they must acquire a minimum lean body mass / body fat ratio prior to dispersal (Nunes and Holekamp, 1996, Nunes, 1998). He also found that the magnitude of this body mass / body fat threshold varied seasonally, with pre-dispersal body fat requirements being low early in the juvenile's active season and increasing gradually as the season progressed. Males able to reach seasonally appropriate body fat levels early in the active season dispersed as juveniles. Males that reached this threshold towards the end of the season delayed dispersal until after their first hibernation. Holekamp (1986) and Nunes et al. (1998) proposed that this body mass / body fat threshold functions to prevent the dispersal of undersized males who would have little chance of surviving the energetic demands of dispersal and hibernation. As a result, dispersal is inhibited at the end of the active season since survival prospects would be slim for dispersing males, regardless of the magnitude of a male's fat stores.

To elucidate the underlying physiological mechanism associated with the onset of dispersal, Holekamp et al. (1985) and Nunes et al. (1999) turned to examining the role of hormones in regulating dispersal behavior. Previous work with other mammals illustrated the importance of pre-natal testosterone in generating sexual dimorphic behaviors (e.g., Phoenix et al., 1959). Since dispersal is male-biased in *S. beldingi*, it was therefore reasonable to assume that testosterone may play a similar role in shaping the dispersal behavior of *S. beldingi*. To test this hypothesis, Nunes et al. (1999) treated neonatal females with testosterone or oil and compared their dispersal behavior to that of untreated males. Their results showed that testosterone-treated, but not oil-treated females exhibited the male-typical dispersal behavior. This result supports the hypothesis that prenatal testosterone is responsible for organizing the neural circuitry necessary to regulate the dispersal behavior of male *S. beldingi*.

In summary, Holekamp and Nunes' work revealed that dispersal in *S. beldingi* is associated with a change in a male's internal environment, the acquisition of a threshold lean body mass/body fat ratio, during the course of an individual's ontogeny. Arrival at this threshold acts apparently on the neural circuitry shaped by prenatal exposure to testosterone, which triggers the onset of a suite of dispersal-related behaviors, including increased locomotor behavior, reduced fearfulness, and dispersal behavior itself (Holekamp, 1986). Hence, their work elucidated the factors that determine dispersal age of male *S. beldingi* at both proximate levels of the Mayr - Tinbergen framework. However, in order to fully explain this behavior it is necessary to reveal the ultimate factors responsible for shaping the observed dispersal dichotomy as well. The objective of this dissertation was to examine the ultimate determinants of dispersal age of male *S. beldingi*.

Evidence from the literature suggests that aggression by local residents towards intruders may prevent the immigration of dispersers, marginalize individuals from resources, and lead to the eviction of recent immigrants (see references in Chapter 2). Furthermore, immigrants exposed to high levels of resident aggression may suffer injuries and are forced into marginal habitat where their survival prospects are slim. Social resistance toward immigrants may therefore have profound fitness consequences for a disperser. As a result, selection should favor dispersal at an age when immigrants pose little threat to local residents, and when the level of aggression directed towards intruders is low.

In the second chapter of this dissertation, I set out own to determine if dispersal age influenced the level of social resistance males encounter during the dispersal process. Differences in the social context of dispersal based on dispersal age suggested that this might be the case. Juvenile dispersers emigrate during a time period when females cease to defend territories and when both males and females are fattening for hibernation. In contrast, yearling dispersers emigrate during the breeding season, when intra- and inter-specific aggression is at its peak. Hence, juvenile dispersal in this species may be adaptive because it reduces the level of aggression males encounter during the immigration process. Using staged- and naturally-occurring encounters, I tested the social resistance hypothesis by examining the responses of adult female and adult male residents towards intruding juvenile and yearling males. I found that resident females aggressively targeted yearling males, while juvenile intruders encountered little female aggression. Adult males, however, direct very little aggression towards juvenile and yearling male intruders. These results indicate

that early dispersal is adaptive by allowing juvenile immigrants to avoid aggression from female residents more effectively than do males who disperse as yearlings.

The persistent bias toward juvenile dispersal also suggests that early dispersal imparts significant survival or reproductive benefits to males that are able to disperse as juveniles. In chapter three, I asked whether dispersal at a young age enhances fitness in male Belding's ground squirrels by increasing male survivorship or mating success. I used live-trapping data to compare the survivorship among males of known dispersal age, and conducted mating observations to assess how dispersal age influenced male mating success. I found that age-specific survivorship differed significantly between early and late dispersers, which was primarily a result of lower juvenile survivorship among males that dispersed as juveniles than for males that delayed dispersal until their yearling summer. My data also showed that juvenile dispersers mated with a greater number of different females than did yearling dispersers. Overall, these results indicate that juvenile dispersal may carry significant survival costs early in life, but ultimately enhances the mating success of surviving males.

To examine the evolutionary origins of dispersal age, I assessed the role of various selective agents in shaping dispersal age among multiple species of ground-dwelling sciurids, including the Belding's ground squirrel (Chapter four). Three hypotheses have been invoked to explain variation in dispersal age among species of this group (see references in Chapter four). The growth limitation hypothesis posits that growth limitations imposed by life history and environmental factors determine dispersal age of ground-dwelling sciurids, and males that are unable to complete sufficient growth during their first active season should delay dispersal until they are older and have acquired sufficient energy resources to support the energetic demands of dispersal. Aggression by local residents can influence immigration success, and the social resistance hypothesis suggests that the need to avoid or counter this aggression may have acted as an important selective agent in shaping dispersal age in sciurids. This hypothesis predicts that, in species where males are likely to encounter social resistance during the immigration and settlement process, individuals should disperse at an older age. Lastly, mortality during transit and early settlement can be high for dispersers, and the risk avoidance hypothesis suggests that risks associated with dispersal may affect the age at which individuals emigrate. This hypothesis predicts that the level of dispersal risk encountered by males of a particular species during dispersal should influence a male's dispersal age. In species where males are exposed to high risks, males should therefore disperse at older ages than in species where males encounter relatively low levels of risks during emigration.

I reviewed the literature on ground-dwelling sciurids for field studies that documented dispersal age and used the extracted data from 22 species to test the predictions of these hypotheses. I found that, relative to adult body mass, the amount of growth males were able to achieve during their juvenile summer had a significant negative effect on the age at which males dispersed, which supports the growth limitation hypothesis. I also observed a positive relationship between the level of social resistance immigrants were likely to encounter and a species' dispersal age, a result that supports the social resistance hypothesis. However, I found no significant relationship between mean dispersal distance, my measure of dispersal risk, and the age at which a particular species generally disperses. This result suggests that a species' dispersal age is independent of the level of risk a male encounters during the dispersal process. However, future work will be necessary to confirm the latter result.

In summary, work by Holekamp and Nunes and the data presented in this dissertation helped to elucidate the factors that determine dispersal age in *S. beldingi* across all four levels of analysis in the Mayr - Tinbergen framework. Studies by Holekamp and Nunes unraveled the ontogenetic basis and physiological mechanisms involved in shaping the observed dispersal dichotomy. They revealed that three factors: body fat, time of year, and testosterone are responsible for shaping the observed dispersal pattern of male *S. beldingi* on a proximate level. My work has focused on examining explanations on the ultimate level by assessing the potential fitness consequences of dispersal age (Chapters two and three) and by determining its evolutionary origin among species closely related to *S. beldingi* (Chapter four). The results presented in chapters two and three suggest that dispersal as a juvenile carries significant fitness benefits by reducing the level of social resistance a male experiences during the immigration process and enhancing male mating success. The comparative study (chapter four) illustrated that juvenile growth and resident aggression have been important selection forces in shaping dispersal age among ground-dwelling sciurids.

APPENDIX. Dispersal ages and summary of variables from the sciurid literature used for comparative analyses.

Species names (GenBank accession number)	[a]Dispersal age (wks)	[b]MI_j	[c]Age at adult body mass (wks)	Effective dispersal distance	Social aggression score	References
C. gunnisoni (AF157930)	24	1	40	2.4	3	Longhurst, 1944; Fitzgerald and Lechleitner, 1974; Rayor, 1984, 1985, 1988; Hoogland, 1985, 2001, 2003; Haynie et al., 2003
C. leucurus (AF157879)	[f]8	1	41	--	1	Tileston and Lechleitner, 1966; Clark, 1977; Hoogland, 1981, 2003
C. ludovicianus (AF157890)	48	0.78	96	25.8	4	Michener and Murie, 1983; Hoogland, 1985, 1986, 1992, 1995, 2001; Garrett and Franklin, 1988; Dobson et al., 1998
M. caligata (AF143920)	100	0.37	146	--	3	Barash, 1975; Barash, 1981, 1989; Holmes, 1984
M. caudata aurea (AF143925)	152	0.37	142	1.5	4	Blumstein, 1997; Blumstein and Foggin, 1997; Blumstein and Arnold, 1998;

[a]Age at which $\geq$50% of males disperse from their natal site (weeks); [b]juvenile maturity index; [c]Age at which males reach minimum adult body mass (wks), [d]one author reported juvenile dispersal in this species (Weddell 1989, 1991); [e]one study reported juvenile dispersal in this species (Webb 1981); [f]authors did not specify exact dispersal ages, and dispersal ages were assigned assuming that males dispersed midway through their juvenile active season.

APPENDIX. Continued.

Species names (GenBank accession number)	[a]Dispersal age (wks)	[b]MI_j	[c]Age at adult body mass (wks)	Effective dispersal distance	Social aggression score	References
M. flaviventris (AF143926)	[d]53	0.51	127	22.3	3	Armitage, 1974, 1975, 1991, 1998; Armitage and Downhower, 1974; Armitage et al., 1976; Svendsen, 1974; Armitage and Johns, 1982; Van Vuren and Armitage, 1994; Van Vuren, 1990; Schwartz et al., 1998
M. marmota (AF100711)	147	0.39	144	3.1	4	Arnold, 1988, 1990a, 1990b, 1993; Arnold and Dittami, 1997; Arnold et al., 1994; Allaine et al., 1998; Hacklander and Arnold, 1999; Goossens et al., 2001
M. monax (AF143934)	4	0.83	105	--	1	Bronson, 1963; Bronson, 1964; Snyder et al., 1961; Merriam, 1971; Ferron, 1988; Barash, 1989; Meier, 1992

[a]Age at which ≥50% of males disperse from their natal site (weeks); [b]juvenile maturity index; [c]Age at which males reach minimum adult body mass (wks), [d]one author reported juvenile dispersal in this species (Weddell 1989, 1991); [e]one study reported juvenile dispersal in this species (Webb 1981); [f]authors did not specify exact dispersal ages, and dispersal ages were assigned assuming that males dispersed midway through their juvenile active season.

APPENDIX. Continued.

Species names (GenBank accession number)	[a]Dispersal age (wks)	[b]MI_j	[c]Age at adult body mass (wks)	Effective dispersal distance	Social aggression score	References
M. olympus (AF111182)	96	0.42	143	--	4	Barash, 1973; Barash, 1989
S. armatus (AF157901)	[f]6	--	98	--	3	Balph and Stokes, 1963; Slade and Balph, 1974; Rieger, 1996
S. beecheyi (AF157918)	4	0.9	87	2.5	1	Evans and Holdenried, 1943; Fitch, 1948; Dobson, 1979, 1983; Dobson and Davis, 1986; Holekamp and Nunes, 1989; Boellstorff and Owings, 1995
S. beldingi (AF157951)	3	0.68	96	1.4	1	Morton et al., 1974; Sherman, 1981a, 1981b; Sherman and Morton, 1984; Holekamp, 1984; Holekamp, 1986; Nunes and Holekamp, 1996; Nunes et al., 1999; Nunes et al., 1998; Nunes et al., 1999

[a]Age at which $\geq$50% of males disperse from their natal site (weeks); [b]juvenile maturity index; [c]Age at which males reach minimum adult body mass (wks), [d]one author reported juvenile dispersal in this species (Weddell 1989, 1991); [e]one study reported juvenile dispersal in this species (Webb 1981); [f]authors did not specify exact dispersal ages, and dispersal ages were assigned assuming that males dispersed midway through their juvenile active season.

APPENDIX. Continued.

Species names (GenBank accession number)	[a]Dispersal age (wks)	[b]MI_j	[c]Age at adult body mass (wks)	Effective dispersal distance	Social aggression score	References
S. citellus (AF157859)	[f]7.5	0.61	91	--	1	Huber et al., 2002; Millesi et al., 1998, 1999; Hoffmann et al., 2003a, 2003b
S. columbianus (AF157939)	[e]52	0.68	95	13.3	1	Murie and Harris, 1978; Murie, 1980; Boag and Murie, 1981; Festa-Bianchet and King, 1984; Wiggett et al., 1989; Dobson, 1992; Waterman, 1992; Wiggett and Boag, 1992, 1993; Boag, 1994; Murie, 1995; but see Weddell, 1989, 1991
S. elegans (AF157891)	5	1	38	0.5	1	Pfeifer, 1982a, 1982b
S. franklinii (AF157893)	[f]6	--	93	--	1	Murie, 1973
S. lateralis (AF157887)	8	0.66	91	--	1	McKeever, 1964; Barnes, 1984; Ferron 1985; Kenagy et al., 1989

[a]Age at which $\geq$50% of males disperse from their natal site (weeks); [b]juvenile maturity index; [c]Age at which males reach minimum adult body mass (wks), [d]one author reported juvenile dispersal in this species (Weddell 1989, 1991); [e]one study reported juvenile dispersal in this species (Webb 1981); [f]authors did not specify exact dispersal ages, and dispersal ages were assigned assuming that males dispersed midway through their juvenile active season.

APPENDIX. Continued.

Species names (GenBank accession number)	[a]Dispersal age (wks)	[b]MI_j	[c]Age at adult body mass (wks)	Effective dispersal distance	Social aggression score	References
S. mollis (AF15798)	4	1	48	1.2	1	Smith and Johnson, 1985; Horne et al., 1997; Olson and Horne, 1998; Antolin et al., 2001
S. parryii (AF157927)	4	0.69	95	3.6	4	Carl, 1971; McLean, 1979; McLean, 1980, 1982; Lacey et al., 1997; Buck and Barnes, 1999; Byrom and Krebs, 1999; Lacey and Wieczorek, 2001
S. richardsonii (AF157915)	4	0.81	100	1.2	1	Michener, 1973; Michener and Michener, 1977; Michener and Sheppard, 1972; Michener and Locklear, 1990; Michener and McLean, 1996
S. tereticaudus (AF157941)	5	1	35	--	1	Reynolds and Turkowski, 1972; Dunford, 1977a, 1977b

[a]Age at which ≥50% of males disperse from their natal site (weeks); [b]juvenile maturity index; [c]Age at which males reach minimum adult body mass (wks), [d]one author reported juvenile dispersal in this species (Weddell 1989, 1991); [e]one study reported juvenile dispersal in this species (Webb 1981); [f]authors did not specify exact dispersal ages, and dispersal ages were assigned assuming that males dispersed midway through their juvenile active season.

APPENDIX. Continued.

Species names (GenBank accession number)	[a]Dispersal age (wks)	[b]MI$_j$	[c]Age at adult body mass (wks)	Effective dispersal distance	Social aggression score	References
S. tridecemlineatus (AF157877)	4	1	41	1.3	1	McCarley, 1966; Schwagmeyer and Brown, 1983; Wistrand, 1974; Schwagmeyer and Woontner, 1985, 1986 Schwagmeyer and Parker, 1987
S. adocetus (AF157844)	--	--	--		--	
S. annulatus (AF157851)	--	--	--		--	

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[a]Age at which $\geq$50% of males disperse from their natal site (weeks); [b]juvenile maturity index; [c]Age at which males reach minimum adult body mass (wks), [d]one author reported juvenile dispersal in this species (Weddell 1989, 1991); [e]one study reported juvenile dispersal in this species (Webb 1981); [f]authors did not specify exact dispersal ages, and dispersal ages were assigned assuming that males dispersed midway through their juvenile active season.

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