Sexual Differences in Reproductive Effort of Richardson’s Ground Squirrels

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SEXUAL DIFFERENCES IN REPRODUCTIVE EFFORT OF RICHARDSON’S GROUND SQUIRRELS

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C. Hart Merriam Presentation

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Male and female Richardson’s ground squirrels exhibit differences in a constellation of behavioral, ecological, and physiological characteristics related to a fundamental sexual difference in reproductive effort, viz. males primarily expend energy on mate acquisition whereas females primarily expend energy on parenting. Male Richardson’s ground squirrels emerge from hibernation earlier than females, at a heavier body mass, and with larger fat reserves. Once females emerge, males reduce time foraging and they compete aggressively and intensively for access to estrous females with resultant physical wounding, loss of body mass, depletion of fat reserves, and high mortality. Females retain post-hibernation fat reserves during gestation and even increase in personal body mass. Although mass of the litter exceeds the mother’s own mass by late lactation, mothers are largely able to meet the demands of milk production through foraging, and their body mass remains fairly constant through lactation. Adult males immerse into hibernation earlier than adult females, and are heavier and fatter on immergence. In their first active season, juvenile males complete growth to adult size, whereas juvenile females attain only 80% of adult size; females then complete growth during pregnancy the following spring. Juvenile males attain adult size by delaying entry into hibernation until 7–9 weeks later than juvenile females. During hibernation, both juvenile and adult male Richardson’s ground squirrels spend substantially less time than females in the physiological state of torpor. In particular, males terminate torpor >1 week before emergence, during which time they subsist on seeds cached in the hibernaculum, replenish fat, and initiate spermatogenesis in preparation for the forthcoming mating season. In contrast, female Richardson’s ground squirrels do not store food in the hibernaculum, they emerge from hibernation <2 days after termination of torpor, and they are impregnated 2–4 days after emergence from hibernation when at their lowest annual body mass. On an annual basis, adult females have a higher survival rate than adult males, largely because females are more likely to survive through the reproductive period.

Key words: *Spermophilus*, annual cycle, body mass, hibernation, lifespan, reproduction, sex ratio, Sciuridae

In 1822, Joseph Sabine named several species of mammals from specimens sent to England by the Arctic Land Expedition which travelled from Hudson Bay to the Arctic Ocean (Houston, 1984). One specimen, collected in May 1820 near Fort Carlton on the North Saskatchewan River, was named *Arctomys richardsonii* as “a tribute to the merits of Dr. John Richardson, who went out with the Expedition as a Naturalist, and to whose attention and care we are indebted for these additions to our zoological knowledge” (Sabine, 1822:590). Sabine conferred the vernacular “tawny American marmot” on this species, but it is now known to zoologists as the Richardson’s ground squirrel (*Spermophilus richardsonii*) and to non-zoologists as the prai-
rie gopher or flickertail (Bell and Piper, 1915; Coues, 1875). My presentation as recipient of the C. Hart Merriam Award is also a tribute, this time to the Richardson's ground squirrels themselves and their endlessly fascinating biology which continues to enrich and enliven my life and career.

Richardson's ground squirrels are semicoxial, diurnally active, obligate hibernators that sleep and hibernate underground but forage above ground in the grasslands of Alberta, Saskatchewan, Manitoba, Montana, North Dakota, South Dakota, and Minnesota (Michener and Koeppel, 1985). Over the past 25 years, I have studied Richardson's ground squirrels at four sites in Canada, one in Saskatchewan (e.g., Michener and Michener, 1977) and the other three in Alberta (e.g., Michener, 1979a, 1989a, 1993a). The data presented here derive primarily from the latter two populations, the first of which (Haney Site) I studied from 1979 until its destruction at the request of the landowner in 1986 and the second of which (Farm Site) I then founded with animals from that extirpated population on a site that had been previously inhabited by this species (Michener, 1996). The principal approach used in my studies has been the collection of longitudinal data, primarily by livestrapping and observation, for the lifetimes of individually identifiable (ear-tagged and dyemarked) animals.

Although Richardson's ground squirrels have been known to mammalogists since the 19th century (Bailey, 1893; Richardson, 1829) and have long been considered agricultural pests throughout the prairies (Bell and Piper, 1915; Brown and Roy, 1943), many basic aspects of their biology were still uncertain or unknown when I commenced my studies in 1969. For example, Howell (1938) estimated gestation length at 28–32 days, whereas Denniston (1957) reported a duration of 17 days for S. [richardsonii] elegans, a species that hybridizes with S. richardsonii (Nadler et al., 1971, 1982). Through an iterative process (Michener, 1977, 1980, 1984a, 1985, 1989b) that involved refining my ability to determine when copulation and parturition occurred underground, I established that neither of these previous estimates was correct and that gestation length for S. richardsonii is 23 days. As additional basic information accumulated from my own work and that of my husband, Dan Michener, on timing of emergence from hibernation (Michener, 1979b), duration of the annual cycle (Michener, 1974), seasonal changes in body mass (Michener, 1974), and annual survival (Michener and Michener, 1971), I perceived that the sexes differ substantially in many aspects of their biology. Subsequently, my research focussed on describing and comparing the behavioral, ecological, and physiological characteristics of male and female Richardson's ground squirrels, with the goal of integrating sexual differences into a coherent picture of the natural history of the species. Here I summarize these sexual differences as they relate to a fundamental difference between the sexes in reproductive effort, namely that male Richardson's ground squirrels primarily expend energy on mate acquisition whereas females primarily expend energy on parenting.

**Reproductive Effort in Mammals**

Mammalian phylogenetic history precludes male mammals from participating directly in gestation and lactation, so males of most species are emancipated from paternal care. Consequently, most male mammals maximize their reproductive success by mating with many females to whom they direct little or no assistance in rearing of offspring. Aside from a suggestion by Davis (1984) that some males alarm call in the vicinity of their lactating mates, Richardson's ground squirrels conform to the typical mammalian pattern in which males gain reproductive success by siring offspring and females by rearing offspring. Individuals likely incur costs in their efforts to reproduce successfully, and those costs can be measured in terms of reduced future reproductive potential or reduced survival.
(Reznick, 1985). A frequent limitation in assessment of survival costs is the difficulty of ascertaining whether missing animals died or dispersed. Because males tend to be the dispersing sex in mammals in general and in ground squirrels in particular (Holekamp, 1984), a sexual difference in dispersal may obscure a sexual difference in survival associated with reproduction. In lieu of determining costs of reproduction in such ultimate terms, costs can be measured in proximate terms, such as loss of mass, depletion of fat reserves, intensity of aggression, and frequency of physical wounding (e.g., Deutsch et al., 1990, 1994). For Richardson's ground squirrels, costs of reproduction differ between males and females, whether measured in proximate or ultimate terms, and the nature of the difference in those costs is revealed in many aspects of the lives of males and females.

**ACTIVE SEASON OF RICHARDSON’S GROUND SQUIRRELS**

**Sexual differences in timing of the active season.**—Male and female Richardson’s ground squirrels differ in the timing of the annual cycle (Fig. 1). The first animals to emerge from hibernation are always adult males, followed 2–3 weeks later by the emergence of adult females. The sexes also differ in timing of immersing into hibernation, but the direction and magnitude of the sexual difference is not the same for adults and juveniles; adult males enter hibernation 1–2 weeks before adult females, whereas juvenile males enter hibernation 7–9 weeks after juvenile females. Due to the staggered emergence and immersing dates, all age and sex classes are simultaneously active in the above-ground population for <2 months each year (Fig. 1). I will use these differences in the annual cycle between age and sex classes as the framework on which to build a discussion of sexual differences in reproductive effort of Richardson’s ground squirrels.

**Time of emergence and mating.**—Yearling and older individuals of the same sex

<table>
<thead>
<tr>
<th>Event</th>
<th>Mean date (n)</th>
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<tbody>
<tr>
<td>1989</td>
<td></td>
</tr>
<tr>
<td>A♂ emerge</td>
<td>24 Feb (24)</td>
</tr>
<tr>
<td>A♀ emerge</td>
<td>22 Mar (94)</td>
</tr>
<tr>
<td>A♀ mate</td>
<td>25 Mar (98)</td>
</tr>
<tr>
<td>Parturition</td>
<td>17 Apr (86)</td>
</tr>
<tr>
<td>Litters emerge</td>
<td>16 May (83)</td>
</tr>
<tr>
<td>A♂ immerge</td>
<td>26 Jun (14)</td>
</tr>
<tr>
<td>A♀ immerge</td>
<td>6 Jul (74)</td>
</tr>
<tr>
<td>J♀ immerge</td>
<td>24 Aug (33)</td>
</tr>
<tr>
<td>J♂ immerge</td>
<td>16 Oct (25)</td>
</tr>
<tr>
<td>1990</td>
<td></td>
</tr>
<tr>
<td>A♂ emerge</td>
<td>21 Feb (59)</td>
</tr>
<tr>
<td>A♀ emerge</td>
<td>8 Mar (151)</td>
</tr>
</tbody>
</table>

**FIG. 1.**—Mean dates of major events in the annual cycle of Richardson’s ground squirrels at the Farm Site in southern Alberta from emergence of adults (≥1 year old) in 1989 to emergence of adults in 1990. Arrows pointing right indicate mean emergence dates and arrows pointing left indicate mean immersing dates. Within the bar, open segments indicate periods when at least one age and sex class is active above ground, the cross-hatched segment indicates the period when all four age and sex classes are simultaneously active above ground, and solid segments indicate all four age and sex classes are in hibernation. Despite differences of 16 weeks between immersing dates of adult and juvenile males and 7 weeks between adult and juvenile females in 1989, juveniles emerged in spring of 1990 as yearlings at similar dates to older members of the same sex; 22 February ± 7 days (SD) for 48 yearling males and 18 February ± 13 days for 11 older males, 8 March ± 5 days for 95 yearling females and 6 March ± 3 days for 56 older females. A = adult, J = juvenile.
Table 1.—Mean dates (SD in days, n) of emergence from hibernation and of estrus for adult (≥1 year old) Richardson’s ground squirrels on the Farm Site in southern Alberta. Feb = February, Mar = March.

<table>
<thead>
<tr>
<th>Year</th>
<th>Male</th>
<th>Female</th>
<th>Male - Female (days)</th>
<th>Estrus</th>
</tr>
</thead>
<tbody>
<tr>
<td>1988</td>
<td>20 Feb</td>
<td>4 Mar</td>
<td>(4, 13)</td>
<td>13</td>
</tr>
<tr>
<td>1989</td>
<td>24 Feb</td>
<td>22 Mar</td>
<td>(9, 24)</td>
<td>26</td>
</tr>
<tr>
<td>1990</td>
<td>21 Feb</td>
<td>8 Mar</td>
<td>(9, 59)</td>
<td>15</td>
</tr>
<tr>
<td>1991</td>
<td>16 Feb</td>
<td>9 Mar</td>
<td>(8, 23)</td>
<td>21</td>
</tr>
<tr>
<td>1992</td>
<td>14 Feb</td>
<td>27 Feb</td>
<td>(10, 27)</td>
<td>13</td>
</tr>
<tr>
<td>1993</td>
<td>21 Feb</td>
<td>9 Mar</td>
<td>(13, 45)</td>
<td>16</td>
</tr>
<tr>
<td>1994</td>
<td>1 Mar</td>
<td>12 Mar</td>
<td>(7, 25)</td>
<td>11</td>
</tr>
<tr>
<td>1995</td>
<td>17 Feb</td>
<td>16 Mar</td>
<td>(12, 9)</td>
<td>27</td>
</tr>
</tbody>
</table>

a Defined as the first day of above-ground activity. Identified by daily censusing of individually dyemarked animals. Excludes immigrants and peripheral animals for whom the first day of activity was not known for certain.

b Defined as the day on which a female mated. For females that copulated on more than 1 day, only the last day of estrus resulting in pregnancy is included.

c Mean dates of emergence for males and females differed significantly in all years (P < 0.001, Student’s t tests).

do not differ significantly in time of emergence (Michener, 1983, 1985), so all animals within a sex are pooled and collectively referred to as adults. Regardless of population size or year, adult male and female Richardson’s ground squirrels differ significantly in the timing of their first above-ground appearance from hibernation; males precede females, usually by 2–3 weeks (Table 1). The sexual difference in time of emergence can be as much as 4 weeks, as occurred in 1989 and 1995 when mild weather during the period of emergence of males in February was followed by prolonged cold weather that delayed the emergence of females. A similar sexual difference in time of emergence of adults from hibernation, with males preceding females, characterizes most species of Spermophilus in North America (Michener, 1984b).

When I recognized that male Richardson’s ground squirrels consistently preceded females above ground in spring (Michener, 1983), I surmised that interpretation of this sexual difference in behavior would benefit from knowledge of when mating occurs relative to when females emerge from hibernation. At that time, information on copulatory behavior was scanty for any species of ground-dwelling squirrel. In the absence of direct information on copulation, my initial approach was to ascertain the reproductive status of females from examination of the external genitalia and inspection of cells obtained in a vaginal lavage. Such physical evidence reveals that estrus is impending when the vulva is enlarged, turgid, pink, and patent, and the vagina is starting to shed cornified epithelial cells. The presence of a copulatory plug or sperm in the vagina on the following day (Michener, 1980, 1984a) confirms that copulation indeed occurred in the preceding 16–24 h. Although Richardson’s ground squirrels usually copulate underground (Michener and McLean, 1996), from those copulations that occur above ground, I have identified a suite of characteristic behaviors shown by consort pairs that can be used to infer the occurrence of underground copulations (also see Davis, 1982). These behaviors include: 1) the female soliciting contact with males, 2) the consort pair retreating underground, usually female first with the male following within 30 s, 3) either or both members of the pair grooming the genital
region on re-emergence, 4) the female re-emerging with a patch of dampened fur on the cheek or neck as a result of being grasped by the male’s mouth, and 5) the male emitting mating calls (a unique vocalization reminiscent of the aerial predator call described by Davis [1984]) either before or after the underground consortship. Underground copulations can likewise be inferred for other species of ground-dwelling squirrels (Boellstorff et al., 1994; Hoogland, 1995; Lacey et al., 1997; Murie, 1995), though details of the diagnostic features differ slightly among species.

Based on physical and behavioral evidence of mating, female Richardson’s ground squirrels are receptive to males for 2–3 h in the late afternoon, most commonly on their second, third, or fourth day out of hibernation (Michener, 1985, 1989b; Michener and McLean, 1996). Even though yearling females are significantly smaller and lighter on emergence than older females (Dobson and Michener, 1995; Michener, 1989b) and are mating for the first time, latency between emergence and estrus does not differ between age classes (Michener, 1985). Regardless of age and year, the majority of females (86–99% annually for 1988–1994 on the Farm Site) are impregnated within 6 days of emergence from hibernation, usually on their first estrus post-hibernation (>90% of females).

Because female Richardson’s ground squirrels have only one litter a year and each female is in estrus for a few hours in the afternoon of one day (or, rarely, 2 or 3 days) a year, reproductive opportunities for males are confined to a short period after females emerge from hibernation. As the mate-limited sex, the reproductive success of males is more at risk from mis-timed emergence from hibernation than is that of females. Thus, I argue (Michener, 1983) that the selective pressure giving rise to the sexual difference in timing of emergence results from the sexual difference in access to mates. Late emergence from hibernation by males is potentially costly in terms of reduced mating opportunities because females that have been above ground for several days would already be inseminated by earlier emerging males. Consequently, the biologically meaningful way to state the sexual difference in time of emergence from hibernation is that males emerge before females, rather than that females emerge after males.

Operational sex ratio and intrasexual competition.—Although male and female Richardson’s ground squirrels are born and weaned in approximately equal numbers, the sex ratio among adult Richardson’s ground squirrels is strongly biased toward females regardless of geographic location, year, or population density (Table 2; Michener and Michener, 1971; Michener, 1989a and references therein). Because females substantially outnumber males (usually by >3:1) and because all females mate, I initially assumed that intrasexual competition among males for access to females would be modest in such female-biased populations. However, two consistent characteristics of males in spring, bodily injuries and loss of mass, obliged me to revise this opinion. Although males initially maintain or even increase in mass post-hibernation, they then lose mass coincident with the mating season (Fig. 2; Michener, 1984c, 1990), indicating that energy expenditure exceeds energy gained through foraging. Lack of suitable forage in March can be rejected as an explanation for the loss of mass by males because females more than meet maintenance costs; indeed, females both increase in personal mass and support growth of embryos (Fig. 2). All males sustain multiple injuries, especially around the face and rump, during the mating season, whereas wounding rarely occurs after the mating season (Michener, 1983; Pellis et al., 1996). Because females are rarely injured at any time in the active season, including the mating season, I surmised that intrasexual aggression among males accounted for the sexual bias in incidence and severity of physical injury. Time and activ-
Table 2.—Sex ratio (females per male) of adult (≥1 year old) Richardson's ground squirrels on the Farm Site in southern Alberta. The total population in spring includes all squirrels present on the study site for at least one day between emergence from hibernation and the day the last female mated. The post-mating population includes males still present the day after the last female mated and females still present at the time of parturition, i.e., the number of animals still resident ca. 4–5 weeks after emergence from hibernation.

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<tbody>
<tr>
<td>Area (ha)*</td>
<td>0.35</td>
<td>0.58</td>
<td>0.86</td>
<td>0.60</td>
<td>0.72</td>
<td>0.71</td>
<td>0.56</td>
</tr>
<tr>
<td>Total population</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Females</td>
<td>55</td>
<td>101</td>
<td>192</td>
<td>103</td>
<td>98</td>
<td>109</td>
<td>79</td>
</tr>
<tr>
<td>Males</td>
<td>16</td>
<td>28</td>
<td>62</td>
<td>32</td>
<td>38</td>
<td>51</td>
<td>28</td>
</tr>
<tr>
<td>Sex ratio</td>
<td>3.4</td>
<td>3.6</td>
<td>3.1</td>
<td>3.2</td>
<td>2.6</td>
<td>2.1</td>
<td>2.8</td>
</tr>
<tr>
<td>Post-mating population</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Females</td>
<td>48</td>
<td>92</td>
<td>166</td>
<td>81</td>
<td>82</td>
<td>88</td>
<td>70</td>
</tr>
<tr>
<td>Males</td>
<td>8</td>
<td>17</td>
<td>34</td>
<td>12</td>
<td>28</td>
<td>24</td>
<td>15</td>
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<tr>
<td>Sex ratio</td>
<td>6.0</td>
<td>5.4</td>
<td>4.9</td>
<td>6.8</td>
<td>2.9</td>
<td>3.7</td>
<td>4.7</td>
</tr>
</tbody>
</table>

* Area inhabited by ground squirrels was calculated as the total number of 10 by 10-m grids with at least one adult female resident in spring. The decline in population density from 1990 to 1994 was associated with predation, particularly by badgers.

...
males, enable them to monitor as many females as possible and to position themselves near estrous females (Michener, 1983; Michener and McLean, 1996; Schwagmeyer, 1990). Males at the Haney Site in 1983 spent about 40% of their above-ground time moving or in alert postures during the mating season compared with about 20% of their time post-mating. Male-male aggression and male-initiated contacts with females were highest during the mating season and collectively accounted for about 13% of above-ground time compared with <4% post-mating. Foraging time was lowest in the mating season, when males spent only 24% of their above-ground time feeding compared with 43% post-mating. Monitoring conspecifics, locating estrous females, and maintaining proximity to estrous females while driving other males away represents a major time and energy commitment for male Richardson’s ground squirrels that is evident in physical terms such as injury and loss of mass.

Behavior of estrous females further com-
Fig. 3.—Numbers of adult (≥1 year old) male and female Richardson’s ground squirrels resident each day within the observation area on the Farm Site in 1994 from late February (when most males emerged from hibernation) to late March (when all females were pregnant). The subset of emerged females that was in estrus each day is indicated by the solid bars. In total, 24 males and 64 females were resident for at least 1 day. Population sex ratio (=number of females per male) was female biased from 10 March onwards, whereas operational sex ratio (=number of estrous females per male) was male biased throughout the mating season.

Complicates male reproductive success. On the day they are in estrus, many female Richardson’s ground squirrels engage in hiding, a behavior that is rarely seen on any other day of the active season and which makes maintenance of proximity to the female difficult for males (Michener and McLean, 1996). When hiding, females appress their ventrum to the ground and lie motionless. Hiding is sometimes followed by slinking, in which the female initially slowly creeps away then assumes the normal running posture to continue moving away from her initial position. This hide-then-run behavioral pattern enables females to move out of their usual home range, often with the result that the female evades contact with one male and moves closer to another male which, in turn, may precipitate aggression between neighboring males as each jockeys for position near to the female. Although female Richardson’s ground squirrels are in behavioral estrus for only 2–3 hours, usually between 1500 h and sunset, over one-half of them mate with more than one male (Michener and McLean, 1996). Electrophoretic analyses (van Staaden et al., 1994) indicate that multiple paternity of a litter can result from mating with several males, so a male’s reproductive success is diluted if he is not the sole mate of a female. Distribution of paternity in multiply sired litters has yet to be ascertained in Richardson’s ground squirrels.

Costs of mating, gestation, and lactation.—During the 2–3 h of behavioral estrus, female Richardson’s ground squirrels spend less time foraging and more time interacting with males and they travel longer distances than during the pre- or post-estrus periods (Michener and McLean, 1996). Consequently, many females fail to increase in mass over the 24 h encompassing mating (Michener, 1984c). This interruption in what is otherwise a pattern of steadily increasing mass from emergence to parturition indicates that some females do incur a brief and minor cost associated with mating.

Typical litter size at birth for Richardson’s ground squirrels in southern Alberta is 6–9 neonates (mean ± SD = 7.7 ± 1.8, range = 4–13, n = 108 captive-born litters; Michener, 1989b). Over 90% of females that lactate subsequently wean a litter, and litter size at weaning usually differs by
Fig. 4.—Litter mass relative to maternal mass (mean ± SD) at 5-day intervals from birth (day 0) to weaning (day 30) for captive-born litters and at birth and first emergence from the natal burrow for field-born litters of Richardson’s ground squirrels. For field-born litters, the mother’s loss of mass over the 2 consecutive days that spanned the time of parturition was used to estimate her litter’s mass at birth. For captive-born litters at all ages and for field-born litters at emergence, litter mass was calculated as the sum of the individual masses of each litter member. Sample sizes indicate the number of litters for which both litter mass and mother’s concurrent mass were known. The dashed line indicates litter mass = maternal mass. Data on captive litters were obtained in 1981, 1982, 1985, and 1986 from litters born to pregnant females removed from the Haney Site in southern Alberta and data on field litters were obtained at the Haney Site from 1982 to 1985 inclusive.

<0.5 young from that at birth in the same year, indicating that most mothers rear all infants to weaning age (Michener, 1989b). Newborn litters weigh about 16% of the mother’s own mass (Fig. 4), but infants increase in mass approximately 10-fold during the next 30 days, such that litters weigh about 157% of the mother’s concurrent mass at first emergence from the natal nest (Michener, 1989b). The collective mass of all the infants in a litter surpasses the mother’s own mass when infants are about 20 days old (Fig. 4).

During gestation and lactation, female mammals must meet maintenance costs and direct energy to embryo growth and to milk production. As a generalization among mammals, gestation is less energetically demanding than lactation (e.g., Randolph et al., 1977), a pattern that holds true for Richardson’s ground squirrels (Michener, 1989b). Indeed, the metabolic costs of gestation are sufficiently modest that yearling female Richardson’s ground squirrels are able to complete growth to adult skeletal size while pregnant (Dobson and Michener, 1995). Furthermore, for both yearling and older females, >50% of the mass gained during pregnancy accrues to the mother herself, such that females weigh significantly more post-partum than at the time of mating (Fig. 2; also see Michener, 1984c; Michener and Locklear, 1990a). In contrast to the substantial increase in personal body mass made during gestation, the mother’s body mass plateaus during lactation (Fig. 2) and females use some of their fat reserves (Michener and Locklear, 1990a). The milk demand imposed by a litter with a collective mass that exceeds the mother’s own mass in late lactation certainly represents a major reproductive expenditure for female Richardson’s ground squirrels.

**Sexual differences in costs of reproduction.**—Daily energy expenditure by golden-mantled ground squirrels (S. saturatus) is somewhat greater for females in late lactation than males during the mating season (Kenagy, 1987; Kenagy et al., 1989). However, because of the behavioral difference in how male and female ground squirrels achieve reproductive success and the temporal difference in when males and females make their major reproductive effort, females are better able to meet the high daily metabolic costs of reproduction through
foraging. Male Richardson’s ground squirrels in southern Alberta experience their highest metabolic demands in March, whereas females make their major reproductive expenditure in late April and early May when temperatures are warmer, day length is longer, and fresh vegetation is abundant. Furthermore, lactating females spend >60% of their above-ground time foraging, whereas mating males forage for <25% of their above-ground time. When costs of reproduction are measured in proximate terms such as loss of mass, depletion of fat, or likelihood of physical injury, parenting effort has lower costs for female Richardson’s ground squirrels than mating effort for males (Michener and Locklear, 1990a).

Costs of reproduction are greater for male than female Richardson’s ground squirrels when measured as probability of remaining resident to the next mating season (Michener and Locklear, 1990a). More specifically, during the 4- to 5-week period following emergence from hibernation, males have a higher probability of disappearing than females (Table 2). Over the 7-year period spanning 1988–1994 at the Farm Site, the average percentage of males that disappeared by the time the last female was impregnated was 46% (27–63%, annually), whereas the average percentage of females that disappeared in an equivalent time period (i.e., before parturition) was 15% (11–22%, annually). Furthermore, females have a high probability of surviving to wean a litter; 82–86% of females at the Haney Site (n = 4 years; Michener and Locklear, 1990a) and 75–90% of females at the Farm Site (n = 7 years) survived the 7–8 weeks that encompass estrus, gestation, and lactation. Probably a portion of the loss of males is due to dispersal before the end of the mating season rather than death, but the large difference in persistence rates between the sexes and the rarity with which adult males immigrate into the population strongly suggest differential mortality associated with reproduction. On an annual basis, about 80% of adult males and 40% of adult females disappear (Michener and Locklear, 1990a), with the result that males rarely live to 3 or 4 years of age whereas females sometimes survive to 5 and 6 years old (Fig. 5; also see Michener, 1989a).

Normally >90% of female Richardson’s ground squirrels rear litters to weaning (Michener, 1989b) but, largely due to badger (Taxidea taxus) predation on litters, about 25% of females failed to wean litters at the Farm Site in 1991. Females that did not wean litters immersed on 6 June ± 8 days (SD), whereas those females that weaned litters immersed significantly later, on 25 June ± 9 days (t = 7.98, P < 0.001, n = 17 females without litters and 49 with litters). Thus, a consequence of successful reproduction for females is delayed immersion, which exposes mothers to above-ground predators for several weeks longer than non-mothers. However, of females alive when litters first emerged in early May 1991, only one of 50 mothers and one of 18 non-mothers disappeared before hi-
**Table 3.**—Mean dates (SD in days, n) of immersion into hibernation for adult (=1 year old) and juvenile (<1 year old) Richardson's ground squirrels on the Farm Site in southern Alberta. Date of immersion was determined for individually dyemarked animals resident on portions of the site where visibility permitted daily censusing of active animals. Aug = August, Sep = September, Oct = October.

<table>
<thead>
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<th>Adults</th>
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<td></td>
<td>Males (n)</td>
<td>Females (n)</td>
<td>Difference&lt;sup&gt;b&lt;/sup&gt; (days)</td>
<td>Males (n)</td>
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<tr>
<td>1989</td>
<td>26 June (14, 14)</td>
<td>6 July (10, 74)</td>
<td>10</td>
<td>24 Aug (14, 33)</td>
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<td>1990</td>
<td>20 June (16, 13)</td>
<td>1 July (9, 48)</td>
<td>11</td>
<td>8 Aug (14, 36)</td>
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<td>1991</td>
<td>28 May&lt;sup&gt;c&lt;/sup&gt; (9, 4)</td>
<td>25 June (9, 49)</td>
<td>28</td>
<td>4 Aug (9, 46)</td>
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<td>1992</td>
<td>5 June (11, 11)</td>
<td>20 June (8, 49)</td>
<td>16</td>
<td>6 Aug (13, 54)</td>
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<tr>
<td>1993</td>
<td>16 June (7, 10)</td>
<td>30 June (14, 37)</td>
<td>14</td>
<td>21 Aug (11, 57)</td>
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<tr>
<td>1994</td>
<td>13 June (11, 12)</td>
<td>29 June (9, 33)</td>
<td>16</td>
<td>4 Aug (12, 22)</td>
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<sup>a</sup> Only females that weaned litters are included.

<sup>b</sup> Mean dates of immersion differed significantly between sexes within an age class (P < 0.01 in all years for adults, P < 0.001 in all years for juveniles, Student's t tests).

<sup>c</sup> An additional adult male with unusually low body mass remained active until 4 September.

bernation, so survival was not reduced as a result of later immersion. For the females that hibernated, over-winter survival did not differ significantly between those that had and had not weaned a litter (63.3% and 70.6%, respectively; χ² = 0.30, P > 0.55). Of these over-winter survivors, more of the females that had weaned a litter in 1991 were still alive 2 months later, in late April 1992 when litters emerged, than females without litters in 1991 (76.5% of 34 versus 58.3% of 12). Thus, weaning a litter did not impair survival either for the remainder of the active season, or over winter, or through the subsequent reproductive period.

Successful reproduction in one season could reduce future fecundity, but no such trend was apparent between females that did and did not wean litters in 1991. Of squirrels still alive at the expected time of litter emergence in 1992, those that had weaned a litter the previous year were more likely than non-weaners to rear another litter to emergence in 1992 (96% of 26 versus 71% of 7) and their litters tended to be larger at first emergence from the natal nest (mean ± SD = 6.0 ± 1.9 for 23 litters versus 4.0 ± 2.9 for four litters), trends opposite to that expected if successful repro-

duction impairs future reproduction. Thus, weaning a litter was not ultimately costly either in terms of survival or future reproductive success for female Richardson's ground squirrels (also see Michener and Locklear, 1990a). Likewise, reproduction by female Columbian ground squirrels (S. columbianus) incurs no detectable costs to survival or future reproduction (Hare and Murie, 1992; Murie and Dobson, 1987; Risch et al., 1995).

**Sexual differences in immersion of adults.**—Once the mating season is over for males and once female Richardson's ground squirrels have weaned litters, the next major event in the annual cycle is entry into hibernation. Both sexes fatten preparatory to hibernation, but adult males begin fattening earlier than do adult females. Adult males attain substantially heavier final masses (Fig. 2) and total fat stores (Michener and Locklear, 1990a), and they enter hibernation about 2 weeks earlier than adult females (Fig. 1, Table 3). On my study sites in southern Alberta, most adult male Richardson's ground squirrels enter hibernation before the summer solstice and most females by early July (Table 3; also see Michener and Locklear, 1990a). Although adult
female and female Richardson’s ground squirrels emerge and immerge at different times, the duration of the active season is similar for the two sexes and lasts about 110 days in southern Alberta (Tables 1 and 3).

Sexual differences in body mass trajectories of adults.—Sexual differences in the behavioral ecology of adult male and adult female Richardson’s ground squirrels during the active season are encapsulated in their body mass trajectories (Fig. 2). Males emerge from hibernation at a heavier mass than females, maintain or slightly increase in mass in the interval before females emerge, but then lose mass during the mating season when they compete for access to females at the cost of reduced foraging time. After the mating season, males increase in mass, initially slowly but then rapidly before the onset of hibernation. For adult female Richardson’s ground squirrels, the main features of the body mass trajectory are an increase in mass between emergence from hibernation and parturition that exceeds the mass invested in embryos and associated extra-embryonic tissues, loss of mass associated with parturition, followed by relatively steady body mass through the 29–30 days that infants spend underground dependent on mother’s milk. Mass increases slightly during the 20–30 days after the litter appears above ground, then females begin to increase in mass more rapidly preparatory to hibernation. One subtle aspect of the body-mass trajectory of females is the 1-day interruption in mass gain on the day of estrus (Michener, 1984c), a cost of mating that is trivial compared with that of males for whom the loss and subsequent recovery of mass back to pre-mating levels spans at least 4 weeks (Fig. 2; also see Michener, 1990; Michener and Locklear, 1990a).

Body-mass trajectories mirror underlying changes in body composition for adult males but not adult females (Michener and Locklear, 1990a, 1990b). Adult males emerge from hibernation with substantial fat stores, deplete fat deposits during the mating season, then store large amounts of energy as fat before hibernation. Females emerge with some residual fat stores, which they retain through gestation but then partially deplete during lactation. Thus, adult males are leanest when their body mass is lowest at the end of the mating season, whereas females are leanest in late lactation but their body mass is lowest on emergence from hibernation.

Sexual differences in immersgence and body mass trajectories of juveniles.—Juvenile male and female Richardson’s ground squirrels are of similar mass at first emergence from the natal nest, but soon thereafter males outweigh females (Fig. 2). Analysis of body composition reveals that the sexes differ in how they partition energy to growth and to fattening during their first summer of life (Michener and Locklear, 1990a, 1990b). Over the 3 months following emergence from the natal burrow, males direct less energy to fattening and more energy to physical growth, as represented by lean dry mass of bone, muscle, and skin, than do females. Thus, at 4 months of age, females are lighter in mass and physically smaller than males, but they have significantly larger fat deposits and are ready to enter hibernation. Juvenile males remain active for an additional 7–9 weeks after juvenile females have immerged (Table 3), during which time they increase further in lean dry mass and deposit fat preparatory to hibernation. Ultimately, juvenile males attain significantly heavier pre-hibernation masses than juvenile females (Fig. 2).

Delayed entry into hibernation relative to juvenile females permits juvenile male Richardson’s ground squirrels to grow to adult size in their first summer of life (Fig. 2). In contrast, juvenile females attain only about 80% of adult size before their first hibernation, then complete growth the following spring while pregnant (Dobson and Michener, 1995). The sexual difference in growth trajectories and time of immersgence of juveniles ensures that yearling males will
be of equivalent size and mass to older males in the mating season. Indeed, yearling males do not differ significantly in body mass from older males on emergence from hibernation whereas yearling females are significantly lighter and smaller than older females (Michener, 1984c; Michener and Locklear, 1990a; Dobson and Michener, 1995).

Both male and female Richardson’s ground squirrels are sexually mature on emergence from their first hibernation as yearlings (when 10–11 months old). Because of the intense male–male competition that characterizes the mating season, yearling males are likely to be reproductively successful only if they are full grown. Because the mating season occurs in March shortly after emergence from hibernation, this growth must occur during the males’ first active season as juveniles. Consequently, males must be born sufficiently early in the year to permit 5–6 months of growth before hibernation. By emerging from hibernation in March in southern Alberta, female Richardson’s ground squirrels ensure that sons have adequate time to grow before their first hibernation so they can be competitive as yearlings in the following mating season. By emerging in February, about 2 weeks before adult females, adult males maximize their opportunities to sire offspring.

Summary of sexual differences in the active season.—As juveniles, male Richardson’s ground squirrels 1) have a longer active season, 2) complete a greater fraction of growth to adult size, and 3) immerse at a heavier mass and greater physical size than females. Compared with adult females, adult male Richardson’s ground squirrels 1) emerge from hibernation earlier, 2) are heavier and fatter at emergence, 3) eat less, fight more, and deplete fat stores during the mating season, 4) lose more mass and over a longer period, 5) sustain more physical injuries, 6) have a lower probability of surviving to summer, and 7) enter hibernation earlier, heavier, and fatter than females.

Hibernation Season of Richardson’s Ground Squirrels

By 1988, my field work with Richardson’s ground squirrels had revealed substantial differences between males and females in attributes such as timing of the active cycle, time and activity budgets, body mass trajectories, and accumulation and depletion of fat reserves. These differences coincide with the sexual difference in timing of maximal reproductive effort which occurs during the mating season in late winter/early spring for males and during the last 2 weeks of lactation in late spring for females. However, Richardson’s ground squirrels spend the majority of their lives in hibernation (Fig. 1). As is typical of other hibernating sciurids (Bakko and Brown, 1967; Kenagy and Barnes, 1988; Morton and Gallup, 1975), male Richardson’s ground squirrels enter hibernation with small abdominal testes but emerge the next spring with large testes descended into a darkly pigmented scrotum (Michener, 1983), leading to the suggestion (Barnes et al., 1986) that males spend a sufficient portion of hibernation at euthermic body temperatures to permit testicular recrudescence. Perhaps the sexual differences that characterize the active season of Richardson’s ground squirrels also extend into the hibernation season. Thus, in the winter of 1988–1989, I began using radiotelemetry to monitor the body temperatures of ground squirrels when sequestered in their hibernacula (Michener, 1992, 1993b) to determine whether males and females partition time between torpor and euthermia differently.

Sexual differences in hibernation patterns.—Richardson’s ground squirrels, like Columbian ground squirrels (S. columbianus—Young, 1990a), hibernate alone. Because ground squirrels curl into a ball with the nose tucked between the hind legs both when asleep and in torpor, a radiocollar with a temperature-sensitive thermistor located on the throat provides a good representation of body temperature. By record-
ing transmitter temperature at least twice daily through the hibernation season, I obtained temperature profiles of Richardson’s ground squirrels in their underground hibernacula (Fig. 6). Large-scale aspects of these temperature profiles are similar for all age and sex classes; body temperature during torpor bouts is similar to concurrent soil temperature, torpor bouts increase in duration as soil temperature declines, longest torpor bouts occur in December and January, and inter-torpor arousals are of short (<24 h) duration. Columbian ground squirrels likewise show a pattern of declining body temperature, lengthening torpor bouts, and short inter-torpor arousals during hibernation (Young, 1990b).

For both Richardson’s ground squirrels (Michener, 1992, 1993b) and Columbian ground squirrels (Young, 1990b), males and females partition time differently between euthermy and torpor. Specifically, during the period spent sequestered in the hibernaculum, males are in the physiological state of torpor for a significantly smaller proportion of time than females. Regardless of age, male Richardson’s ground squirrels spend 85% of the time sequestered in the hibernaculum in torpor compared to 91% for females (Michener, 1992, 1993b). Nontorpid intervals occur 1) between entry into the hibernaculum and the first torpor bout (=post-immersion euthermy), 2) between consecutive torpor bouts (=inter-torpor arousal), and 3) between terminal arousal from the final torpor bout and emergence from the hibernaculum (=pre-emergence euthermy). All three intervals are longer for males than females, significantly so for inter-torpor arousals and pre-emergence euthermy (Michener, 1993b), with the latter contributing most to the sexual difference in time spent euthermic while in the hibernaculum. Many (12/23) male Richardson’s ground squirrels were euthermic for ≥6 days, some (n = 6) for as long as 15–25 days, whereas the pre-emergence euthermic intervals of females (n = 13) were always <2 days. Because males both terminate tor-

Fig. 6.—Torpor patterns of Richardson’s ground squirrels hibernating in natural hibernacula on the Farm Site in southern Alberta in 1989–1990, based on twice-daily records of body-surface temperature obtained from radiocollars. One representative individual from each of the four age and sex classes is shown. Arrows indicate the days on which each squirrel im-merged and emerged. Soil temperature was obtained from the Agriculture Canada Research Station, Lethbridge, 16 km S of the study site. Redrawn from Michener (1992).
por many days in advance of emergence and then emerge from hibernation earlier than females, the pre-emergence euthermic interval begins in late January–early February for males in southern Alberta, when soil temperatures are coldest.

**Sexual differences in hibernaculum caches.**—Maintenance of euthermia while sequestered in a cold hibernaculum is metabolically expensive, raising the questions of how males meet the costs of thermoregulation and why males expose themselves to this energetic cost. Even though male Richardson’s ground squirrels spend more time euthermic during hibernation than females, they lose a smaller proportion of their pre-hibernation mass and they lose less mass per day spent euthermic in hibernation (Michener, 1992), suggesting that males meet the costs of prolonged pre-emergence euthermia through means other than depletion of fat. Indeed, males with the longest periods of pre-emergence euthermia in a cold hibernaculum lose the least mass over winter (see Michener, 1993b:112, figure 1), a relationship that makes sense only if males have access to food stores in the hibernaculum. Incidental observations during the active season suggested that males were more likely than females to gather seeds in their cheek pouches, a pattern I confirmed by provisioning grain. Males rapidly removed such food bonanzas by repetitively taking loads of grain underground in their cheek pouches, whereas females ate the grain at the provisioning site or removed grain for immediate consumption elsewhere (Michener, 1993b).

Determination of whether the seeds that are taken underground by males are cached in the hibernaculum for use during hibernation (rather than stored in sleeping chambers for more immediate use, say overnight), requires knowledge of the location and contents of an individual’s hibernaculum. Richardson’s ground squirrels normally do not sleep in the hibernaculum until they have sequestered themselves for the hibernation season (Michener, 1992), so the functional criterion for distinguishing the hibernaculum from the numerous sleeping chambers used by an individual squirrel is that the hibernaculum is the site where the animal becomes torpid. To obtain information on hibernaculum contents would thus require digging up the torpid animal and, in the process, destroying its hibernaculum. I was reluctant to do many such excavations, but a resident badger obligingly excavated and killed 14 radiocollared squirrels shortly after they emerged and I supplemented these data with an additional seven excavations (Michener, 1993b). Whereas none of 8 females had seeds cached in the hibernaculum, 10 of 13 males had caches (range = 60–1736 g dry mass). The same trend was apparent in hibernacula I excavated after emergence of squirrels in spring; no females (0/14) had evidence of caches, whereas most males (9/14) had residual caches (range = 233–1079 g; two additional males had small remnant caches of 2 g and 9 g). Collectively, the information on hibernaculum contents reveals a marked sexual difference in presence of seed caches in concordance with behavioral observations on the propensity to cache.

The hibernaculum chambers of both male and female Richardson’s ground squirrels are spherical, filled with dry grass as bedding material, and located at an average ± SD depth of 57.2 ± 13.9 cm (range = 34.0–101.5 cm, n = 47 chambers measured from the midpoint of the chamber to the soil surface; Michener, 1992, 1993b). Hibernaculum chambers used by males are larger in diameter than those of females (Michener, 1993b), in part because males are larger at emergence (Fig. 2) and in part because of the storage space required for seeds; three of eight males whose hibernaculum contents were measured in autumn had >1,220 g dry mass of seed cached in the chamber.

**Role of hibernaculum caches.**—The presence of a food cache increases the likelihood that a male will have a prolonged period of pre-emergence euthermia that is
accompanied by low over-winter loss of mass (Michener, 1993b). Males with caches usually are euthermic for ≥6 days before emergence and lose mass at <6 g per euthermic day, whereas all females and those males without caches are euthermic for ≤4 days pre-emergence and lose mass at a greater rate. Although not confirmed directly, the logical interpretation of the inverse relationship between time euthermic pre-emergence and loss of mass is that the longer a male can consume cached food the greater the opportunity to replenish the body reserves that were used during heterothermy, especially during periodic rewarming. Thus, one presumed advantage of pre-emergence euthermity is preparation for the forthcoming mating season by building up fat reserves that can then be used to subsidize the costs of mating activity. A second advantage of pre-emergence euthermity is that it permits testicular recrudescence. Biopsies from testes of newly emerged males in spring (Michener, 1992) confirmed this prediction; males that had been euthermic for >11 days had spermatogenesis advanced to the stage of spermatozoa in the seminiferous tubules, whereas males euthermic for <4 days had few spermatids and no spermatozoa.

Because most males spend many days euthermic before emergence above ground, the sexual difference in time of emergence is underlain by an even greater difference in time of terminal arousal from torpor. For example, amongst radiocollared Richardson’s ground squirrels in 1990, males appeared above ground 17 days before females, but they terminated torpor 27 days before females (Michener, 1992). Spermatogenesis and increases in body mass can occur both in the 1- to 3-week interval between termination of torpor and emergence from hibernation and in the 2- to 4-week interval between emergence from hibernation and commencement of the mating season.

Summary of sexual differences in the hibernation season.—Regardless of age, male Richardson’s ground squirrels 1) spend a smaller proportion of the hibernation season in torpor, 2) spend more time euthermic between termination of torpor and emergence from the hibernaculum, 3) lose less mass per euthermic day, and 4) are more likely to have seeds cached in the hibernaculum than females.

Concluding Comments

Returning to the sexual differences in the timing of the annual cycle of Richardson’s ground squirrels (Fig. 1) and in body mass trajectories (Fig. 2), we can now appreciate that these are reflections of the sexual differences in how males and females direct their energy towards attaining reproductive success. By immersing later than juvenile females, juvenile males essentially complete growth to adult size in preparation for intrasexual competition during the mating season the following spring. By emerging earlier than females in spring, yearling and older males can prepare physically and physiologically for the appearance of the first estrous females. In contrast to males, female Richardson’s ground squirrels are under much less selective pressure to be large and fat at the time of mating. Instead, they use the 4-week interval between emergence from hibernation and parturition to build up body mass, including completion of skeletal growth if yearling. Females time emergence to ensure access to lush green forage when in the late stages of lactation 6–8 weeks post-emergence, whereas males time emergence to ensure access to mates.

Sexual differences in behavioral and physiological ecology of Richardson’s ground squirrels during hibernation form a continuum with the sexual differences evident in the active season, and they likewise reflect the difference between males and females in partitioning of reproductive effort. During hibernation, females minimize energy expenditure by spending little time at euthermic body temperatures and they depend exclusively on fat reserves to meet these energy demands. In contrast, by terminating torpor up to sev-
eral weeks before emergence from hibernation, males incur the costs of euthermy while still sequestered in a cold hibernaculum, but these costs are met through access to seeds cached in the hibernaculum. Food caching precedes hibernation and hibernation precedes mating, so males can be viewed as preparing for the next mating season as much as 7–10 months in advance by caching seeds in the current active season to meet future costs of euthermy, fat replenishment, and testicular growth while in the hibernaculum.

Though I have gained many fascinating insights into the lives of Richardson’s ground squirrels in the past 25 years, much still remains to be learned. Regrettably, few mammalogists have selected this species for studies of behavioral and physiological ecology. Compared with rodents such as _Peromyscus_ and _Microtus_, ground-dwelling squirrels have a number of attributes to commend them as research subjects, including greater visibility, larger size, diurnal activity, and a tendency to live in open habitats. I trust that this summary of sexual differences in the behavior, ecology, and physiology of Richardson’s ground squirrels will serve to interest another generation of mammalogists in studies of the rich Nearctic sciurid fauna, particularly the prairie-dwelling _S. richardsonii_.

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**LITERATURE CITED**

**BAILEY, V.** 1893. The prairie ground squirrels or spermophiles of the Mississippi Valley. United States Department of Agriculture, Division of Ornithology and Mammalogy Bulletin, 4:1–69.


**BELL, W. B., and S. E. PIPER.** 1915. Extermination of ground squirrels, gophers and prairie dogs in North Dakota. North Dakota Agriculture Experiment Station Circular, 4:1–11.


**HARE, J. F., and J. O. MURIE.** 1992. Manipulation of litter size reveals no cost of reproduction in Colum-


RICHARDSON, J. 1829. Fauna Boreali-Americana; or the zoology of the northern parts of British America: containing descriptions of the objects of natural history collected on the late northern land expeditions, under command of Captain Sir John Franklin, R. N.


