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Original Research

# Demography and Life History of a Manitoba, Delta Marsh Population of Franklin's Ground Squirrels (*Poliocitellus franklinii*)

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## Abstract

Concerns over population declines and disappearances persist for Franklin's ground squirrels (*Poliocitellus franklinii*) throughout the American Midwest, yet little is known about even basic aspects of this species' ecology. We live-trapped a free-living population of Franklin's ground squirrels near Delta Marsh, Manitoba over the course of 4 years. We analyzed population demographics and life history traits, including adult density and sex ratio, adult survival, adult growth and fecundity, as well as juvenile mass, litter sex ratio and recruitment to the yearling age cohort. Seasonal patterns of mass change for maternal and non-maternal females and males in Delta Marsh population of this obligatorily hibernating species were similar across seasons and largely consistent with those reported among other Franklin's ground squirrel populations. Adult females (≥1 year) outnumbered adult males by roughly 2:1, while litter sex ratio at juvenile emergence was consistently close to 1:1 in this population. Maternal females at our Delta Marsh site had a lower average litter size (6.31) than reported elsewhere for Franklin ground squirrels, and juvenile males weighed more than females at emergence. Survival varied between sexes and among years in the Delta Marsh population. Low survival between 2000 and 2001 followed detrimental agricultural practices and flooding, and subsequently led to a sharp population decline in 2001. The population eventually crashed in 2004 but rebounded by 2014. While population disappearances fuel concern over Franklin's ground squirrel population status in the Midwest, apparent losses may reflect periodic fluctuations typical of this species' demography, or population relocation rather than loss proper.

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**Key Words**: Demography, Franklin's Ground Squirrels, Life History, *Poliocitellus franklinii*, Population Fluctuations.

# INTRODUCTION

As population dynamics are fundamentally determined by a population's vital rates, management and conservation decisions often rely upon information about an organism's life history (Saether *et al.* 1996a; Sibly and Hone 2002; Oli and Dobson 2003; Krebs 2009). Life history and demographic traits determine a population's finite growth rate, which is used widely by managers in population monitoring and modeling (Winemiller and Rose 1992; Saether *et al.* 1996b; Beston 2011), while seminal theoretical works of Cole (1954) and Lack (1954) delved into evolutionary aspects of life history. Knowledge of life history traits, as influenced by mechanisms of population regulation (Charlesworth 1980; Kawecki and Stearns 1993), is thus central to both population and evolutionary biology, and of interest to wildlife managers and ecological theorists alike.

Ground squirrels generally make ideal subjects for demographic studies given the relative ease with which individuals are trapped, marked, and observed in open habitats (Smith and Johnson 1985; Dobson 1995; Hoffmann *et al.* 2003). The study of Franklin's ground squirrels (*Poliocitellus franklinii*), however, has been impeded by the species' preference for densely vegetated habitats (Haberman and Fleharty 1971; Krohne *et al.* 1972; Huebschman 2007). Franklin's ground squirrels tend to occupy areas between woodland-field or woodland-marsh ecotones where woody scrub and tall grass are prevalent, thus obscuring direct observation and complicating trapping (Sowls 1948; Haberman and Fleharty 1971; Jones *et al.* 1983; Martin and Heske 2005). Field study is further hindered by the species' "secretive" nature (Krohne *et al.* 1972), "semi-nomadism" (Jones *et al.* 1983), and limited time spent above ground, even compared to other hibernating sciurid species (Sowls 1948). As such, while long-term demographic and life history studies are readily available for many ground squirrel species, particularly from North America (Slade and Balph 1974; Dunford 1977; Michener and Michener 1977; Boag and Murie 1981; Sherman and Morton 1984; Smith and Johnson 1985; Sherman and Runge 2002), accounts remain relatively scarce for Franklin's ground squirrels (Iverson and Turner 1972; Murie 1973).

Demographic and life history data are particularly important for Franklin's ground squirrels as concerns over the species' population status exist throughout the southern and eastern reaches of the species' range (Pergams and Nyberg 2001). Franklin's ground squirrels typically occur at low densities throughout the American Midwest, and north through the aspen parkland region of Canada (Huebschman 2007). Though the species is reported to occur locally at high densities (Cassola 2016), reports of population declines, crashes, and disappearances have warranted concern for the species throughout much of its range. Currently, Franklin's ground squirrels are considered threatened in Illinois (Illinois Endangered Species Board 2015), endangered in Indiana (Indiana Department of Natural Resources 2013), imperilled to vulnerable in Missouri (Missouri Department of Conservation 2016), and imperilled in Wisconsin (Wisconsin Department of Natural Resources 2014). While apparent population declines and habitat loss drive concerns in these areas, a more complete knowledge of the species' life history and basic ecology is required for accurate population assessment and any future management plans (Lewis and Rongstad 1992; Johnson and Choromanski-Norris 1992; Martin *et al.* 2003; Huebschman 2007).

We conducted a demographic study of a Franklin's ground squirrel population located near Delta Marsh, Manitoba, less than 10 km southwest of the beach ridge utilized by Sowls (1948) during his pioneering natural history investigation of the species over a half century ago. We summarize and report population demographics and life history traits, including adult density and sex ratio, adult survival, adult growth, and fecundity, as well as juvenile mass and litter sex ratio. As this population was investigated over the years leading up to a population crash, the population parameters and life history traits compiled here also lend insight into wide-ranging population declines that have prompted concern over the species' status across its range.

# MATERIAL AND METHODS

### Study area and animals

Research on Franklin's ground squirrels was conducted from the start of May to the start of August in 1998–2000, and from 8 May through 26 May, and 30 June through 15 July, in 2001 at 50°9'N, 98°21'W near Delta Marsh, Manitoba, Canada. The study site consisted of an approximately 1-km$^2$ area comprised of hayfield, crop fields, mixed deciduous forest, marsh edge and rural roadsides (for details of the geology, biogeography, and ecology of the area, see Love and Love 1954; Shay 1999).

Franklin's ground squirrels are obligate hibernators. In Manitoba, males emerge from hibernacula as early as the end of April, 1-2 weeks before females. Mating occurs from the time of female emergence in early May through early June, and yearlings can breed (Sowls 1948; Iverson and Turner 1972). Gestation lasts 28 d (Choromanski-Norris *et al.* 1986) and lactation lasts up to 31 d (Turner *et al.* 1976). Adult males immerge to hibernacula as early as late July, followed by adult females in late August, and juveniles may remain active above ground as late as early October (Sowls 1948; Iverson and Turner 1972).

**Trapping and handling of squirrels**

We trapped Franklin's ground squirrels using National and Tomahawk (Tomahawk Live Trap, Tomahawk, Wisconsin, USA) live traps baited with peanut butter and rolled oats. We covered all traps with corrugated plastic to protect ground squirrels from overheating in intense sun. Upon initial capture in the season, we marked all squirrels with a unique metal ear tag (Monel #1, National Band & Tag Co., Newport, Kentucky, USA) for permanent individual identification and with a unique dye mark on their dorsal pelage for visual identification (Clairol Hydrience™ Pearl Black #52, Procter and Gamble Co., Stamford, Connecticut, USA). We checked traps hourly to limit animal stress and re-applied dye marks as needed throughout the season. Upon each capture, we weighed squirrels to the nearest 5 g (Pesola™ spring scale, Baar, Switzerland) and assessed reproductive status.

We assessed squirrels for reproductive status and assumed breeding date based on observation of genitalia as described by Murie and Harris (1982). We estimated parturition based on a 28 d gestation period (Choromanski-Norris *et al.* 1986) and observed weight loss >40 g over a 24-h period. We thereafter estimated juvenile emergence based on a 31-d lactation period (Turner *et al.* 1976), and began more intensive monitoring of nests so as to trap young of the year soon after emergence from their natal burrow. We sexed, marked, and weighed all juveniles upon capture, and typically completed full litter assessment within 5 d of their initial emergence. These methods followed the guidelines of the American Society of Mammalogists (ASM) (Sikes *et al.* 2011), and were approved by the institutional animal use and care committee of Brandon University (1998–1999: protocol number 1997R02-2/3), the University of Manitoba (1999–2001: protocol number F99-041) and Manitoba Conservation (verbal permission from Larry Bidlake, Western Regional Office).

**Data summary and analyses**

Bi-weekly mass measurements were summarized for adult (≥1 year) males, maternal females (litter-producing), and non-maternal females (no evidence of lactation as judged by nipple status and failure to produce litter) across the trapping period within each year. Mean mass values for individuals were included in population-wide mass averages whenever more than one mass measurement was taken for a single individual over the bi-weekly period. We included only resident squirrels (considered as individuals trapped on site during at least 2 bi-weekly periods) in adult sex ratio, mass, and population density summaries as well as overwinter survival estimates. Only litters confidently assessed within 5 d of initial juvenile emergence were included in juvenile mass analyses, and all confidently assessed litters were included in summaries of litter size, litter sex ratio (proportion of males to total litter size), and dates of initial juvenile emergence. Breeding dates for maternal females were estimated by backdating from the date of litter emergence based on the aforementioned gestation and lactation period durations, and corroborated with observations of copulatory plugs resembling those described for Columbian and Arctic ground squirrels by Murie and McLean (1980) or evidence of semen in the vaginal area of trapped females during the breeding season.

Adult sex ratio (F:M) was examined during each season as well as each bi-weekly trapping period for all resident squirrels in that there was no indication of sex-differential trappability of the marked individuals in our Franklin's population. Adult overwinter survival was calculated between years (1998–1999, 1999–2000, and 2000–2001) as the proportion of resident adults that were trapped in the final 3 trapping periods (26 June – 6 August) and trapped again the following season. As losses may also represent emigration from the site, this calculation represents minimum adult survival. Similarly, we calculated yearling recruitment between the years 1998–1999 and 1999–2000 as the proportion of juveniles tagged following natal emergence in the summer that were subsequently recaptured the next year following spring emergence. Here recruitment includes non-dispersing and surviving juveniles.

Data were assessed for normality and homoscedasticity using Shapiro-Wilk normality tests and Levene's tests, respectively, as well as visual inspection of the data. We compared all litter variables (litter emergence date, litter size, juvenile mass, litter sex ratio) among years using one-way ANOVAs, with the exception of average breeding dates as these values were backdated from dates of litter emergence and thus share an identical distribution. We compared average adult mass values within each group (adult males, adult maternal females, and adult non-maternal females) among years for each bi-weekly period using one-way

ANOVAs. We compared average male and female juvenile masses within litters using paired *t*-tests, and compared adult male and maternal female masses within each bi-weekly period using two-sample *t*-tests. Summary values are reported as mean ± SE. All statistics were performed using R software (version 3.0.2, R Development Core Team 2013). We report actual significance levels from statistical tests except where $P$<0.001, where we simply report that range.

## RESULTS

Within adult males and maternal females, average mass differed among years during only 1 trapping period (males: 12 June – 25 June, one-way ANOVA, $F_{2,19}$ = 4.267, $P$=0.029; maternal females: 26 June – 09 July, one-way ANOVA, $F_{3,40}$ = 2.971, $P$=0.043), and thus all seasons were ultimately pooled. Small sample sizes among seasons prohibited seasonal comparisons for non-maternal females. Excepting a decline between the periods comprising late lactation (29 June – 23 July), maternal females gradually gained weight between all bi-weekly periods encompassed by the trapping seasons (Table 1). Adult males lost weight only between the 2 initial trapping periods of the season (1 May – 28 May), and experienced the sharpest increase in mass leading up to the end of trapping late in the season (10 July – 6 August; Table 1). Non-maternal adult females experienced an average weight increase between all bi-weekly periods throughout the trapping season. While non-maternal females tended to be lighter than maternal females upon spring emergence (maternal: 345.00 ± 52.134 g; non-maternal: 262.50 ± 67.175 g), they had a greater average mass than females that had reared a litter at the end of the season (maternal: 425.29 ± 36.040 g; non-maternal, $n$ = 1, 585g). Average mass for adult males differed from adult maternal females in only 2 trapping periods (1 May – 14 May and 10 July – 23 July; Table 1).

The average date of initial juvenile emergence occurred within the first 10 d of July for all years (Table 2), and thus estimated breeding dates for maternal females across all seasons occurred within the first 2 weeks of May, coinciding with observations of copulatory plugs and evidence of semen in the vaginal areas of females trapped at that time (James Hare, 2015, University of Manitoba, unpublished data). While litter size did not differ among years (one way ANOVA, $F_{3,38}$ = 1.331, $P$=0.278), the lowest average litter size occurred in 1999, and the highest occurred in 2001 (Table 2). Average litter sex ratio at juvenile emergence was also similar across years (one-way ANOVA, $F_{3,38}$ = 1.137, $P$=0.347), and the pooled average approximated parity (Table 2). Average juvenile mass at emergence differed among years (one way ANOVA, $F_{3,31}$ = 9.267, $P$<0.001); however, post-hoc comparisons using Tukey's HSD tests indicated that among all years, only the 1999 season differed from the 2000 season (1999 = 99.11 ± 5.403 g, 2000 = 66.60 ± 3.836 g, two-sample *t*-test: $t_{26}$ = 4.907, $P$<0.001), and thus years were ultimately pooled (average juvenile mass = 83.17 ± 3.349 g, $n$ = 35 litters). Within litters, average juvenile male mass was greater than average juvenile female mass at emergence (paired *t*-test: males = 85.18 g, females = 81.26 g, $t_{28}$=1.724, $P$=0.048).

Table 1. Comparisons using 2-sample *t*-tests of average mass for adult maternal female (litter producing) and adult male resident ground squirrels (present in at least 2 bi-weekly periods) within each bi-weekly period at the Delta Marsh site from 1998–2001. Values are reported as mean ± SE. Sample sizes were insufficient to compare between sexes in the 24 July – 6 August period.

| Period | Reproductive Period | Female Mass (g) | Male Mass (g) | df | *t* | *P* |
|---|---|---|---|---|---|---|
| 1 May - 14 May | Breeding | 345.00 ± 11.66 | 389.93 ± 10.60 | 33 | -2.755 | 0.01 |
| 15 May - 28 May | Gestation | 397.36 ± 5.96 | 388.00 ± 8.48 | 62 | 0.929 | 0.357 |
| 29 May - 11 June | Gestation | 400.14 ± 5.42 | 413.52 ± 8.99 | 57 | -1.356 | 0.18 |
| 12 June - 25 June | Lactation | 413.06 ± 5.12 | 425.05 ± 7.58 | 56 | -1.359 | 0.18 |
| 26 June - 9 July | Lactation | 429.80 ± 5.26 | 444.04 ± 11.42 | 65 | -1.298 | 0.199 |
| 10 July - 23 July | Post juvenile emergence | 424.54 ± 7.30 | 491.64 ± 31.34 | 38 | -3.64 | < 0.001 |

Table 2. Summary of average litter emergence dates, litter sizes, and litter sex ratios for maternal (litter producing) female Franklin's ground squirrels that were resident (present in at least 2 bi-weekly periods) at the Delta Marsh site from 1998–2001. Only litters in which all juveniles were confidently assessed are included in the analyses. Mean emergence date differed among years (one-way ANOVA, $F_{3,38} = 20.150$, $P<0.001$) and thus values were not pooled. Values are reported as mean ± SE, *n* = litters.

| Year | *n* | Juvenile Emergence Date ± days | Litter Size | Sex Ratio |
|---|---|---|---|---|
| 1998 | 5 | 5 - July ± 0.812 | 6.60 ± 0.510 | 0.39 ± 0.082 |
| 1999 | 17 | 10 - July ± 0.992 | 5.53 ± 0.637 | 0.53 ± 0.066 |
| 2000 | 14 | 1 - July ± 0.520 | 6.64 ± 0.476 | 0.39 ± 0.070 |
| 2001 | 6 | 8 - July ± 1.342 | 7.50 ± 1.176 | 0.58 ± 0.153 |
| Pooled | 42 | --- | 6.31 ± 0.357 | 0.475 ± 0.042 |

Adult females outnumbered adult males in this population by at least 2:1 for >90% of the observed bi-weekly trapping periods throughout the study period, while the operational sex ratio (OSR) of breeding females to males during the breeding period ranged from 1.3:1 in 2001 to 2:1 in 1998 and 1999 (Table 3). Adult survival within the population, reflecting losses attributable to dispersal as well as mortality, varied unpredictably between sexes by as much as 13% (Table 4), and survival of both sexes varied extensively among years (Table 4). The lowest overwinter survival for both sexes (males: 11%, females: 24%; Table 4) occurred between 2000–2001 following a high-speed disc harrow agricultural event during lactation in 2000 and early spring overland flooding in 2001 (James Hare, 2015, University of Manitoba, personal observation). Female juvenile recruitment exceeded male juvenile recruitment in both the 1998–1999 and 1999–2000 seasons (Table 5).

# DISCUSSION

Reports of seasonal mass cycles are commonplace for populations of hibernating ground squirrel species (Morton 1975; Knopf and Balph 1977; Boag and Murie 1981; Fagerstone 1988; Buck and Barnes 1999). Franklin's ground squirrel maternal females gained the most weight during early gestation, while they gained the least weight or lost weight between periods encompassing parturition in early June and the end of lactation in late July, respectively. Females in this population experienced less prominent periods of weight loss following parturition and the energetically demanding period of lactation than among Franklin's ground squirrel populations elsewhere (Iverson and Turner 1972; Murie 1973; Choromanski-Norris *et al.* 1986). This may reflect either better conditions and ample resource availability during our study, which allowed females to quickly regain mass following parturition and partially compensate for increased energetic demands placed on females during lactation (Kenagy *et al.* 1989; Rogowitz 1996), or that smaller observed litter sizes at our Delta Marsh site (see below) buffered females from possible high costs of reproduction that would have produced a more pronounced weight loss. Though the sample of confirmed non-maternal females on this site was small and necessitates cautious interpretation, the data garnered here indicate that non-maternal females are able to gain more weight throughout the season than maternal females who are burdened with the energetic and nutritional costs of reproduction. Consistent with reports of Franklin's ground squirrel populations elsewhere (Iverson and Turner 1972; Murie 1973; Choromanski-Norris *et al.* 1986), males within the Delta Marsh population lost mass only during the period coinciding with breeding early in the season, wherein males endure costs of finding and competing for mates (Sowls 1948).

Across all years, average litter size on our site was less than that reported for Sowls' (1948) Delta Marsh site, or elsewhere in the species' range (Haggerty 1968; Iverson and Turner 1972; Murie 1973). However, Sowls (1948) and Iverson and Turner (1972) occasionally used embryo counts and placental scars to assess litter size; thus, the lower litter sizes observed at our Delta Marsh population may reflect losses between parturition and juvenile emergence rather than differences in reproductive output as documented for other small mammal species (northern pocket gophers, *Thomomys talpoides*; Proulx 2002). At emergence, males weighed more than their female littermates, and continued to be heavier than females through their active season. Such male-biased sexual dimorphism at the time of juvenile

Table 3. Total number and sex ratio (SR) of adult male and adult female resident squirrels (present in at least 2 bi-weekly periods) trapped within each bi weekly period and entire trapping season from 1998–2001 at the Delta Marsh site. Figures in parentheses represent maternal (litter producing) females. SR is calculated as the proportion of females to males within each period.

| Period | Reproductive Period | 1998 Females | 1998 Males | 1998 Sex Ratio | 1999 Females | 1999 Males | 1999 Sex Ratio | 2000 Females | 2000 Males | 2000 Sex Ratio | 2001 Females | 2001 Males | 2001 Sex Ratio |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 May - 14 May | Breeding | 8 (4) | 2 | 4.0 (2.0) : 1 | 1 (1) | 2 | 2.0 (2.0) : 1 | 18 (11) | 8 | 2.3 (1.4) : 1 | 5 (4) | 3 | 1.7 (1.3) : 1 |
| 15 May - 28 May | Gestation | 12 (6) | 5 | 2.4 (1.2) : 1 | 15 (13) | 7 | 2.1 (1.9) : 1 | 21 (14) | 10 | 2.1 (1.4) : 1 | 7 (6) | 3 | 2.3 (2.0) : 1 |
| 29 May - 11 June | Gestation | 12 (7) | 4 | 3.0 (1.8) : 1 | 17 (14) | 8 | 2.1 (1.8) : 1 | 22 (15) | 11 | 2.0 (1.4) : 1 | -- | -- | -- |
| 12 June - 25 June | Lactation | 11 (8) | 4 | 2.8 (2.0) : 1 | 16 (14) | 8 | 2.0 (1.8) : 1 | 21 (14) | 10 | 2.1 (1.4) : 1 | -- | -- | -- |
| 26 June - 9 July | Lactation | 13 (10) | 6 | 2.2 (1.7) : 1 | 14 (13) | 8 | 1.8 (1.6) : 1 | 21 (15) | 7 | 3.0 (2.1) : 1 | 6 (6) | 2 | 3.0 (3.0) : 1 |
| 10 July - 23 July | Post juvenile emergence | 12 (10) | 6 | 2.0 (1.7) : 1 | 2 (2) | 1 | 2.0 (2.0) : 1 | 11 (9) | 5 | 2.2 (1.8) : 1 | 5 (5) | 2 | 2.5 (2.5) : 1 |
| 24 July - 6 Aug | Post juvenile emergence | 2 (1) | 2 | 1.0 (0.5) : 1 | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| Seasonal | | 18 (10) | 7 | 2.6 (1.4) : 1 | 19 (16) | 9 | 2.1 (1.8) : 1 | 26 (15) | 12 | 2.2 (1.3) : 1 | 7 (6) | 3 | 2.3 (2.0) : 1 |

Table 4. Minimum overwinter survival for adult male, adult female, maternal female (litter producing), and adult non-maternal female (non-lactating and confirmed non littering) Franklin's ground squirrels at the Delta Marsh site for 1998–2001. Only resident squirrels (trapped in at least 2 bi-weekly periods) and those individuals captured within the final 3 bi - weekly trapping periods (26 June–6 August) are included in minimum survival estimates. Survival was calculated as the proportion of resident adults that were trapped in the final three trapping periods (26 June–6 August) and trapped again the following season (see Methods for further survival estimation procedure).

| Year | Males | | All Females | | Maternal Females | | Non-Maternal Females | |
|---|---|---|---|---|---|---|---|---|
| | Survival | *n* | Survival | *n* | Survival | *n* | Survival | *n* |
| 1998 - 1999 | 83% | 6 | 69% | 13 | 70% | 10 | 50% | 2 |
| 1999 - 2000 | 36% | 8 | 38% | 16 | 33% | 15 | 100% | 1 |
| 2000 - 2001 | 11% | 9 | 24% | 21 | 14% | 14 | 0% | 2 |
| Pooled | 39% | 23 | 40% | 50 | 36% | 39 | 40% | 5 |

emergence, which persists through adulthood, is also observed in Richardson's ground squirrels (Ryan *et al*. 2012; Gedir and Michener 2014) and is both common, and most pronounced among the rodents for ground squirrels (Schulte-Hostedde 2007), where competition among males for estrus females presumably selects for increased male body size (Andersson 1994; but see Matějů and Kratochvii 2013).

Adult females outnumbered males in this population across most trapping periods by roughly 2:1, while the primary litter sex ratio annually approximated parity. Adult female bias in sex ratio is characteristic of many ground squirrel species, which is largely attributed to increased male losses during male-biased dispersal typical among ground-dwelling squirrels (Schmutz *et al.* 1979), though some species exhibit a more pronounced sex ratio bias than that documented here (McCarley 1966; Dunford 1977; Michener and Michener 1977; Bronson 1979; Dobson 1979). Demographic investigations of Franklin's ground squirrels to date report a 1:1 adult sex ratio (Iverson and Tuner 1972; Murie 1973), leading to the suggestion of distinctive differences in dispersion and social organization of Franklin's ground squirrels relative to their North American congeners (Murie 1973). The female biased adult sex ratio observed here, however, fits the typical ground squirrel pattern generated by male biased dispersal and thus fails to support the contention that Franklin's ground squirrels exhibit a unique social

Table 5. Recruitment of the previous season's female and male Franklin's ground squirrel juveniles to the yearling age cohort at the Delta Marsh site in 1999 and 2000. Spring flooding in 2001 prevented viable estimates of recruitment for that year.

| Year | Juvenile Males | | Juvenile Females | |
|---|---|---|---|---|
| | Recruitment | *n* | Recruitment | *n* |
| 1998 - 1999 | 6% | 35 | 15% | 48 |
| 1999 - 2000 | 18% | 60 | 42% | 48 |

structure based upon population sex ratio. In addition to female-biased recruitment to the yearling age cohort evident in our study, there is some evidence that Franklin's ground squirrels exhibit characteristic male-biased juvenile dispersal in the fall (Martin and Heske 2005). Our data are limited to only 2 years, and cannot discern survivorship from dispersal, while Martin and Heske's (2005) study relied on only 5 individuals (1 male and 4 females) that were followed to hibernation, with individuals of both sexes sometimes traveling distances in excess of 1 km. Further investigation is necessary to elucidate any relationship between population sex ratio and dispersal, as well as the underlying social organization in Franklin's ground squirrels.

Overwinter survival and population density within this population varied extensively and unpredictably between sexes and among years. Male survival peaked at 83% between 1998 and 1999, and fell to just 11% between 2000 and 2001. Though not as extreme as adult males, adult female survival likewise peaked between 1998 and 1999 at 69%, and fell to nearly 24% between 2000 and 2001. The high survival estimates observed between 1998 and 1999 for both sexes are higher than values reported in any other Franklin's ground squirrel population, corroborating the notion that favourable site conditions prevailed during those years. The low survival between 2000 and 2001 and subsequent population decline observed in 2001 following a catastrophic agricultural event and a high-water table indicate that local conditions have a pronounced influence on population abundance at this site. A high-water table likewise contributed to high mortality within a population of Richardson's ground squirrels in Saskatchewan (Proulx 2012), further demonstrating the influence of stochastic flooding events on ground-dwelling sciurids. While an ultimate crash in the Delta Marsh population 3 years later (2004; James Hare, 2015, University of Manitoba, unpublished data) remains uninvestigated, the population rebounded by 2014, enabling a detailed investigation of nest relocation behaviours (James Hare and Ellen Pero, 2015, University of Manitoba, unpublished data). Sowls (1948) reported 4-6-year cyclic population declines at Delta Marsh, and, in the absence of obvious variation in predation pressure, suggested climatic extremes as one of many possible mediating factors. Though spatially asynchronous, population cycles have also been purported to occur elsewhere across the range of Franklin's ground squirrels (Minnesota: 10-yr cycles, Erlien and Tester 1984). While multiannual periodic population fluctuations are rare for mammalian species (Sinclair 2003), cycles are characteristic and often pronounced in some small mammal species and in populations at higher latitudes, particularly among microtine rodents and lagomorphs (Elton 1942; Krebs and Myers 1974; Keith 1990; Norrdahl 1995; Stenseth *et al.* 1997). Potential factors mediating population cyclicity in Franklin's ground squirrels include climatic stochasticity and agricultural events (this study; Sowls 1948), population motility (Martin *et al.* 2003), predation, and disease (Erlien and Tester 1984). The aforementioned factors remain speculative, highlighting the need for long-term population level studies to garner data that reflect the mode and mechanisms of population regulation in Franklin's ground squirrel populations.

The population decline observed within this population over a relatively short period of time does not necessarily indicate a population trend and cannot address the question of population cyclicity. However, the decline here mirrors population crashes and disappearances prevalent among Franklin's ground squirrel populations in the Midwest, many of which are not evidently associated with cycles (Johnson and Choromanski-Norris 1992; Martin *et al.* 2003; Huebschman 2007). Under the assumption that Franklin's ground squirrels are a prairie-obligate species, some researchers attribute population declines to loss of tall grass prairie habitat by mowing, grazing, or cultivation (Johnson and Choromanski-Norris 1992; Pergams and Nyberg 2001). However, categorizing Franklin's ground squirrels as a prairie-obligate species may be erroneous (Huebschman 2007; Duggan *et al.* 2011), and thus factors driving declines remain equivocal. In addition, measures of population viability and persistence (e.g. minimum population levels, Shaffer 1981) remain uninvestigated for Franklin's ground squirrel populations, yet are crucial for assessing accurate population status where declines are of concern.

In summary, the mass cycles observed for groups of maternal and non-maternal females and males in the Delta Marsh population were similar across years and largely consistent with those reported for other Franklin's ground squirrel populations. Adult females outnumbered adult males by roughly 2:1, while litter sex ratio at juvenile emergence was consistently around 1:1 in this population. Maternal females at the Delta Marsh site had a lower average litter size (6.31) than reported elsewhere for Franklin ground squirrels, and juvenile males weighed more than females at emergence. Survival varied between sexes and among years, with low survival between 2000 and 2001 following harmful agricultural practices and flooding leading to a sharp population decline in 2001. While population disappearances fuel concern over Franklin's ground squirrel population status in the American Midwest (Indiana Department of Natural Resources 2013; Wisconsin Department of Natural Resources 2014; Illinois Endangered Species Board 2015; Missouri Department of Conservation 2016), apparent losses may reflect periodic fluctuations typical of this species' demography, or population relocation rather than loss (Pero 2015). Long-term data further elucidating population dynamics and viability remain sorely required for this species

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