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Abstract

Hibernation is a key life history feature that can impact many other crucial aspects of a species' biology, such as its survival and reproduction. I examined the timing of hibernation and reproduction in the federally endangered New Mexico meadow jumping mouse (*Zapus hudsonius luteus*), which occurs across a broad range of latitudes and elevations in the American Southwest. Data from museum specimens and field studies supported predictions for later emergence and shorter active intervals in montane populations relative to low-elevation populations. A low-elevation population located at Bosque del Apache National Wildlife Refuge (BANWR) in the Rio Grande valley was most similar to other populations of *Z. hudsonius*: the first emergence date was in mid-May and there was an active interval of 162 days. In montane populations of *Z. h. luteus*, the date of first emergence was delayed until mid-June and the active interval was reduced to ca 130 days, similar to some populations of the western jumping mouse (*Z. princeps*). Last date of immergence into hibernation occurred at about the same time in all populations (mid to late October). Evidence suggests that females may have a single litter per year in montane populations. At BANWR two peaks in reproduction were expected based on similarity of active season to *Z. h. preblei*, but the population exhibited little detectable above-ground activity in August, which could stem from a failure of the population to produce early litters. Recommendations are made with respect to appropriate timing of surveys for *Z. h. luteus*.

Key words: hibernation, life cycle, activity season, reproduction, New Mexico meadow jumping mouse, *Zapus hudsonius luteus*

Introduction

The meadow jumping mouse (*Zapus hudsonius*) is considered a profound hibernator, meaning that it does not eat during brief arousals from hibernation, and it has one of the longest hibernation periods of any mammal (Whitaker 1972). This long period of hibernation is a key natural history attribute that influences many other important aspects of the species' biology (Kirkland and Kirkland 1979, Turbill et al. 2011). Hibernation is advantageous because survival rates tend to be higher during hibernation than during the active season, presumably due to reduced exposure to predators (Meaney et al. 2003, Turbill et al. 2011, but see Schorr et al. 2009). However, recovery from hibernation, reproduction, and gain in fat to enter and survive the next hibernation all must happen within a brief active period during the warmer months. Timing of emergence from hibernation influences subsequent timing of reproduction, number of litters possible, timing of entrance into hibernation (i.e., immergence), and ultimately overwinter survivorship (Muchlinski 1988). As detailed below, timing of emergence from hibernation is cued by soil temperature, while timing of immergence into hibernation is cued, at least in part, by photoperiod; together, these result in a variable but short active season that constrains potential reproduction.

In jumping mice, emergence from hibernation in the spring is cued by soil temperature (Cranford 1978, Muchlinski 1988, French and Forand 2000). Studies of *Z. hudsonius* from the eastern U.S. have demonstrated that males emerge at lower soil temperatures than females and hence males are active above ground prior to females (Muchlinski 1988, French and Forand 2000). In *Z. hudsonius* from Ingham County, Michigan, first emergence of females averaged 14 days after first emergence of males, and the mean date of emergence of females was 17 days later than males (data from Muchlinski 1988). Timing of emergence in *Z. hudsonius* is known to vary annually and geographically due to variation in soil temperature (Quimby 1951; Muchlinski 1988). Similarly, timing of emergence from hibernation in the western jumping mouse (*Z. princeps*), which occurs in the Rocky Mountain region, also is cued by soil temperature (Cranford 1978) and hence it varies with elevation (Brown 1967, Cranford 1983). In Wyoming, emergence of *Z. princeps* occurred approximately 2 weeks later for each 305 m increase in elevation (Brown 1967), but Cranford (1983) also observed considerable variation due to habitat quality and other local features such as aspect and shade. Female *Z. princeps* in Wyoming emerged 9 to 12 days later than males (Brown 1967), but Cranford (1983) found that timing of emergence in Utah was uniform except at the highest elevations.

Evidence suggests that photoperiod cues immergence into hibernation by *Zapus hudsonius* in the eastern U.S. (Neumann and Cade 1964, Muchlinski 1978, 1980b). Because timing of immergence is cued by photoperiod, entrance into hibernation by adult *Z. hudsonius* may be more uniform both geographically and annually, in comparison to emergence. Hibernation is preceded by a critical ca 2 week period of rapid (e.g., 8% per day) weight gain (Quimby 1951, Morrison and Ryser 1962, Muchlinski 1988). In the eastern U.S., adults undergo weight gain during late August and all have entered hibernation by about the end of the first week in September (Muchlinski 1988). Adult males enter hibernation first, followed by adult females; juveniles enter hibernation last with timing dependant on birth date (later litters entering hibernation as late as October; Muchlinski 1988). In contrast to *Z. hudsonius* from the eastern U.S., hibernation in *Z. princeps* was cued by availability of seeds in the diet rather than photoperiod (Cranford 1978). It has been hypothesized that this difference is a strategy that allows *Z. princeps* to cope with a much shorter period of above ground activity in the high elevation sites it occupies (i.e., ca 2.7 - 4 months as compared with ca 5.5 months in many eastern U.S. populations of *Z. hudsonius*; Cranford 1978, 1983, Muchlinski 1980b). During years with late spring emergence and plant growth, jumping mice might not have enough time to accumulate pre-hibernation fat if immergence was consistently cued by day length. Consequently, cueing on availability of seeds is thought to allow *Z. princeps* to initiate hibernation when conditions are most favorable (Muchlinski 1980b).

One of the main constraints of a short activity season is the number of litters that can be produced annually. Mating apparently occurs soon after the females have emerged from hibernation (Whitaker 1972) and hence timing of spring emergence influences the time available for females to raise young to weaning and then for young of the year jumping mice to mature and ultimately gain fat in preparation for hibernation. Variation in emergence times has resulted in litters being produced 2-3 weeks later in some years (Muchlinski 1988). Gestation is 18-21 days (Quimby 1951) and it then requires ca 4 weeks after birth before the young are weaned and become independent (Whitaker 1972). It required ca 90 days for a juvenile jumping mouse to attain the mass of 20 g, which is adult size (Quimby 1951). Preparation for hibernation then requires a 2-week period of fattening (Morrison and Ryser 1962). Thus, the minimum time required from conception to hibernation in *Z. hudsonius* is ca 125 days. In the eastern U.S. the active interval (i.e., number of days from emergence of the first animal in the spring to the immergence of the last animal in fall) is ca 162-165 days (Muchlinski 1988). Evidence suggests that female *Z. hudsonius* must achieve a large body mass in order to reproduce, which can result in delays in reproduction (Falk and Miller 1987). Thus, some females produce their first litter within a month after emergence (i.e., early breeding females), while females that did not breed during the first month may produce a litter during the second month after emergence (i.e., late breeding females; Quimby 1951). In the eastern U.S., both early and late breeding females may produce a second litter and there is some evidence that lactating females can become pregnant and that young of early litters may breed (Quimby 1951). Hence, in the eastern U.S. there are two (sometimes three) peaks in reproduction during the active season and females may produce two and possibly three litters per year (Quimby 1951, Whitaker 1963, Nichols and Conley 1982). A similar pattern was observed for *Z. h. preblei*, which occurs along the Front Range of southeastern Wyoming and Colorado, but it has a shorter active season (150 days) and two peaks in reproduction (Meaney et al. 2003). In *Z. princeps*, females that emerge from hibernation with low body weights (i.e., young of prior breeding season) are more likely to delay reproduction and have smaller litters (Brown 1967, Falk and Millar 1987). Compared to other demographic groups, young of late litters must extend their activity season later into the Fall in order to gain weight; even so, these young ultimately have lower survival likely due to a longer period of exposure to predators and lower body weights when entering hibernation (Muchlinski 1988, Meaney et al. 2003, Schorr et al. 2009).

Zapus h. luteus is a well-differentiated form that is endemic to the American Southwest, including portions of southern Colorado, New Mexico, and central and eastern Arizona (Hafner et al. 1981, Frey 2012, Malaney et al. 2012). *Zapus h. luteus* is a specialist of riparian habitats and hence its distribution includes both low elevation sites within desert biomes and high elevation sites within coniferous forest biomes (Frey and Malaney 2009, Malaney et al. 2012). The known distribution of *Z. h. luteus* extends between 32.7° N and 37.2° N latitude and between 1,375 m and 2,926 m elevation, possibly as low as 935 m (i.e., Camp Verde, Yavapai County, Arizona; Frey 2008, 2012). Given the large size and extreme topographic variability of this region, *Z. h. luteus* is expected to exhibit geographic variation in timing of emergence from hibernation and possibly immergence into hibernation. For instance, it has been suggested that *Z. h. luteus* may not hibernate in the middle Rio Grande valley (i.e., Valencia and Socorro Counties; Morrison 1988, Najera 1994, Najera et al. 1994). Thus, the purpose of ~~this research~~ was to determine the timing of hibernation and reproduction in *Z. h. luteus* and to compare these data with other taxa of jumping mice. I predicted for *Z. h. luteus* that: 1) emergence from hibernation will be later for higher latitudes and higher elevations due to overall cooler climate and hence cooler soil temperatures in Spring; 2) immergence into hibernation will be later for lower latitudes and lower elevations due to longer growing seasons; 3) the active interval will be shorter for montane populations as opposed to valley populations, and 4) the number of litters possible will be reduced for montane populations. I also report an apparent unusual midsummer hiatus in above ground activity by *Z. h. luteus* at Bosque del Apache National Wildlife Refuge (BANWR), which is the lowest elevation site known to be currently occupied by the taxon.

Information about timing of hibernation is important because other facets of natural history, such as numbers of litters possible, are dependent on activity season. However, there also are practical reasons for needing information on activity season of Z. *h. luteus*. Due to substantial declines in populations over the last several decades, *Z. h. luteus* was listed as endangered under the U.S. Endangered Species Act in June 2014 (USFWS 2014). Consequently, compliance surveys for this taxon will become necessary for certain projects within the species' range and it is essential that such surveys be conducted when the species is active above ground since there is no reliable way of detecting presence of hibernating jumping mice.

Methods

I examined ~~and synthesized~~ all relevant data available for *Z. h. luteus*, which included information from throughout the known range of the taxon (see Malaney et al. 2012). This included all known museum specimens of *Z. h. luteus* with recorded dates of capture (N = 309). Specimens were in the following collections: Academy of Natural Sciences of Philadelphia (ANSP; N = 10), Arizona State University Mammal Collection (ASUMC; N = 6); Denver Museum of Natural History (DMNH; N= 14); Frey Tissue (FT; N = 63), University of Kansas, Museum of Natural History (KU; N=5), Museum of Northern Arizona (MNA; N = 7); University of New Mexico, Museum of Southwestern Biology (MSB; N = 118); University California, Berkeley, Museum of Vertebrate Zoology (MVZ; N = 11); New Mexico Museum of Natural History and Science (NMMNHS; N = 2); New Mexico State University, Vertebrate Collection (NMSU; N = 6); San Diego Natural History Museum (SDNHM; N = 25); Museum of Texas Tech University (TTU; N = 1); University of Arizona, Collection of Mammals (UA; N = 9); University of Illinois Museum of Natural History (UIMNH [collection transferred to MSB]; N = 6), University of Utah, Utah Museum of Natural History (UMNH; N = 7), United States National Museum (USNM; N = 18); Western New Mexico University (WNMU; N

= 1). Wherever possible, I further refined information by supplementing specimen data with information on field studies from published literature and unpublished reports.

Because soil temperature is influenced by elevation and latitude, I categorized specimens into nine populations divided into two groups: montane (N = 242; Sangre de Cristo Mountains, Jemez Mountains, Sacramento Mountains, White Mountains) and low elevation valley (N = 67; Florida River, Sambrito Creek, Mora River, Rio Chama, Rio Grande). I constructed histograms of numbers of specimens of each sex by Julian date to evaluate times of emergence from and immergence into hibernation. I examined timing of emergence according to relative temperature equivalents of locations. To a large extent, the climate of a location is ultimately based on its latitude and elevation (i.e., higher latitudes and higher elevations have cooler temperatures). Consequently in order to compare locations that vary in latitude and elevation I calculated a temperature equivalent for the locations based on the method described in Frey et al. (2007). The temperature equivalent was set in relation to a hypothetical location located 34°N latitude, 1,981 m (6,500 feet) elevation with a mean annual temperature of 12.2°C (54°F), which are approximate averages for New Mexico. The temperature lapse rate was set to 0.56°C (1°F) per 1° latitude and per 76 m (250 feet) elevation. The temperature equivalent for a location was calculated: TE = 54 + ([(6,500 - elevation in feet)/250] + [34-degrees latitude]).

To establish timing of reproduction the primary data I used was evidence of pregnancy, usually via counts of embryos recorded on specimen tags because these data are unequivocal. I found inconsistencies in the recording of pregnancy in field data. Consequently, for field data I only considered females as pregnant if they were recorded as pregnant and there was some other data corroborating pregnancy such as excessive body mass (> 22 g), which is consistent with late pregnancy (Quimby 1951, Meaney et al. 2003). I did not consider specimen tag data on lactation reliable because "lac" may be recorded for females in a variety of conditions such as swollen mammae or post-lactation. I used specimen data on reproductive condition of males only to supplement the pregnancy data because data on scrotal versus nonscrotal testes were sparse. I used a 21-day gestation period (though gestation actually may vary from 18-21 days), a 28-day ~~nesting~~ period (time from parturition to weaning and independence), and growth rates for young of the year animals to back-calculate dates of conception and parturition, though it is cautioned that back-calculated dates based on mass of juveniles are often overestimated (Quimby 1951).

For museum specimens, I examined cranial and dental characters when possible to establish relative age. Specimens were assigned to 1 of 6 age classes according to wear on the cheekteeth as described by Krutzsch (1954) and specimens were assigned to 1 of 8 age classes based on eruption and wear on the third upper molar (M3) and closure of the basioccipital-basisphenoid suture according to Jones (1981). The Krutzsch (1954) and Jones (1981) age classes for a specimen were transformed into fractions of the total age class possible (e.g., a Krutzsch age class 4 = 4/6 = 0.66). Following Frey (2008), the age class was the mean of the two fractions for an individual. An age class of ca 0.2 was interpreted as corresponding to recently weaned juveniles, while age class 0.35 was inferred to be in their second active season.

Results and Discussion

Emergence from hibernation

Emergence from hibernation was earlier for some valley populations than montane populations (Figure 1). The earliest captures represented by the specimens were 3 males on 24 May from the Rio Grande valley population (Isleta Pueblo; 34.9° N latitude, 1,495 m elevation). However, field studies recorded slightly earlier dates. Further south along the Rio Grande at Bosque del Apache National Wildlife Refuge, Socorro County (BANWR; 33.8° N latitude, 1,370 m elevation), Najera (1994; see also Zwank et al. 1997) trapped for *Z. h. luteus* beginning in March 1992, but did not capture a jumping mouse until 13 May. Males made up 83% of captures during May with the first female caught on 20 May (Najera 1994). The report of a capture on 13 March by Zwank et al. (1997) is an error (see Table 15 and Appendix B in Najera 1994). During another study at BANWR in 2009 - 2011, the earliest captures were two males on 18 May 2010, but the first female that year was not caught until 18 June (Wright 2012, Frey and Wright 2012). During the previous year, trapping started 21 May with a male caught on 22 May and the first female caught on 26 May; over both years 78% (N = 9) of jumping mice caught in May were male. The earliest capture date for a valley specimen outside the middle Rio Grande valley were two females caught 24 June at Espanola, Rio Arriba County, New Mexico (36.0°N latitude, 1,700 m elevation).

No specimens from montane areas have been captured in May (Table 1). The earliest capture represented by specimens from montane areas was a male caught 11 June at Sugarite Canyon, Las Animas County, Colorado (37.0°N latitude, 2,300 m elevation; Jones 1999). Earliest dates of specimens in other well-sampled montane populations include 18 June (Sacramento Mountains: Tularosa Creek, Otero County, 33.1°N latitude, 2,050 m elevation), 20 June (White Mountains: West Fork Black River, 33.8°N latitude, 2,330 m elevation), and 28 June (Jemez Mountains: San Antonio Creek, Sandoval County, 35.9°N latitude, 2,355 m elevation). Of 12 montane specimens with June capture dates and gender data, only 4 were females, which were taken 18, 27, 29, and 30 June. Morrison (1987) conducted the only field study that attempted to determine timing of emergence in a montane population at Fenton Lake in the Jemez Mountains, Sandoval County, New Mexico (35.9° N latitude, 2,350 m elevation). Her first capture was a male on 13 June with the first female not captured until 27 June (Morrison 1987). She caught a total of 14 males and 1 female during June (Morrison 1987).

The relationship between temperature equivalents of locations and known first emergence dates predicted that for each degree increase in temperature equivalent the emergence date would occur almost two days earlier (Figure 2). Dates of earliest known museum specimens from specific locations often were later than predicted, likely due to small sample sizes and because specimens were collected incidentally without special attempt to determine emergence date. Predicted dates of *first* emergence for key populations of *Z. h. luteus* extend over 49 days from 6 May to 24 June (Table 2). It should be noted that variation will exist around these predicted dates due to small sample sizes, coarse nature of the model, and annual and site-specific variation in soil temperature.

Immergence into hibernation

Among specimens from low elevation valley locations, none had capture dates after 16 September (Table 1, Figure 1). Data on age class revealed that older age classes had disappeared by 4 September, while most young animals had disappeared by 16 September (Figure 3). However, field studies reveal later dates of immergence. During a 7 – 19 September trapping period in the Rio Chama and Rio Grande valleys near Espanola, Rio Arriba County, Morrison (1988) caught two adult males with weights (31.5 g and 37.0 g) that are typical of adult jumping mice imminently ready to enter hibernation. At BANWR, Najera (1994) and Zwank et al. (1997) caught jumping mice through September and until 22 October, though all were young of the year in these months except an adult female (24.0 g) on 12 September and an adult male that weighed 32.0 g on 27 September and 35.0 g on 1 October, and was eminently ready for immergence (Table 3). Wright (2012) did not catch any jumping mice at BANWR in September, but caught a 20.0 g young of the year female on 22 and 25 October. This jumping mouse was radio-collared and its last above ground movement was 26 October (Wright 2012). *Z. hudsonius* is known to occasionally arouse from hibernation, perhaps due to accumulation of metabolic waste products or loss of potassium from nerve and muscle tissues (Muchlinski 1980a). No jumping mice have been detected at BANWR between 27 October and 13 May, despite 1,740 trap-nights (1 trap-night = 1 trap set for 1 night) by Najera (1994) in March, April and November and an effort of 7,540 trap-nights during relatively warm days throughout this period (Wright and Frey 2010; Wright 2012). Thus, jumping mice at BANWR do hibernate and the population had an active interval of 162 days (= ca 5.5 months) in 2010 (Wright 2012).

Among specimens from montane locations, only 14% were captured after August (Table 1). Of specimens of known age, the last recorded date was 19 September (Figure 3). However, three specimens of unknown age class were caught in October, including 4, 19, and 26 October, all from the White Mountains, Arizona (Table 1). At Fenton Lake, Morrison (1987) caught 5 jumping mice in October that previously had been captured with the last caught on 3 October after which trapping ended. Morrison (1987) thought that most adults had entered hibernation by mid-September and that later occurrences were young of the year. However, immergence of adults into hibernation could occur earlier. In *Z. h. preblei* some adults were imminently ready for hibernation in the third week in August (Meaney et al. 2003). The active interval for montane populations cannot be as precisely determined, but is ca 124 – 135 days (ca 4 to 4.5 months) for Fenton Lake (13 June to probably mid-October).

Problems Interpreting Reproduction During Field Studies

Najera (1994) and Wright (2012) reported jumping mice of all ages, including juveniles and pregnant females, during May at BANWR. However, evidence suggests that ~~interpretation is~~ incorrect. First, while some field studies of jumping mice have used body mass as an indicator of age (e.g., Brown 1967, Nichols and Conley 1982), body mass is highly variable within individual jumping mice and overwintered adults can emerge from hibernation with relatively low body mass (< 20 g) in May and June (Quimby 1951, Meaney et al. 2003). As an example, Wright (2012) captured a jumping mouse that was unequivocally a juvenile (7 g and juvenile pelage) on 16 August 2009. This animal was recaptured the following spring on 18 May 2010, at which time it weighed only 14 g, which equates to a 60 day old juvenile (Quimby 1951)! Hence, body weight alone cannot be used to determine age, at least in the early part of the active season (Meaney et al. 2003).

Second, evidence suggests that some field evaluations of pregnancy may be inaccurate. For instance, Wright (2012) reported capturing 9 females that were evaluated as pregnant (Supplemental Table 1). Of those, 7 had excessive body weight (> 22 g; Meaney et al. 2003) or enlarged mammae that corroborated pregnancy. In addition, 7 were radio-tracked. Three exhibited normal activity behaviors during the radio-tracking session, which consisted of nightly foraging in herbaceous wetland habitats and nesting during the day in above-ground nests in grasses (Wright and Frey in press). In contrast, four exhibited dramatically different behaviors that were interpreted as tending a maternal nest with nursing young, although the possibility that these females had entered hibernation cannot be discounted. These females left the typical wetland habitats and became almost entirely inactive for ca 2 or more weeks in underground burrows located in woody habitats devoid of herbaceous vegetation. A similar burrow used by an adult female *Z. h. preblei* contained fetuses (Ryon 2001). Importantly, no females captured in May, and recorded as pregnant, had corroborating evidence of pregnancy. Therefore, it is possible that fat layers remaining from hibernation made the females appear pregnant when they were not. Consequently, field evaluations of pregnancy should be suspect without corroborating information such as swollen mammae, palpated fetuses, excessive weight, or behavioral changes.

Reproduction at BANWR

The most well studied population of *Z. h. luteus* is at BANWR. At this location, most pregnancies occur in late June and July. Wright (2012) caught females with corroborating evidence of pregnancy on 23 June, and 20, 25, 26, and 27 July (Supplemental Table 1). For radio-collared jumping mice, parturition dates probably coincided with retreat to underground burrows on 28 and 30 July (Supplemental Table 1). Hence, back calculated conception dates are 7 and 9 July, and juveniles from those litters would be weaned and become part of the trappable population on 25 and 27 August, respectively. There may be some variation in these dates because some of the radio-collared pregnant jumping mice had unusual and reduced activity just prior to retiring in the underground burrows and it is conceivable that they gave birth outside the burrows and then moved the young or conversely they retired to the burrow just prior to giving birth. Data from Najera (1994) support late June through July as the primary period for pregnancy at BANWR. A 29.0 g female that appeared pregnant on 9 July but that was recaptured at least 7 days later (no date given) and appeared to be no longer pregnant but lactating (Najera 1994). Females captured that were evaluated as both pregnant and with large body mass (> 22 g) included two on 15 July 1991 (25.0 and 29.0 g), and one each on 27 June 1992 (28.0 g), 8 July 1992 (22.5 g), 9 July 1992 (29.0 g), and 16 July 1992 (26.0 g) (Najera 1994).

The earliest date of pregnancy recorded at BANWR is a 21.5 g female was captured on 15 June 2014 that was confirmed pregnant through palpation of embryos and presence of enlarged nipples (BANWR 2014). Two additional female jumping mice (23.5 g and 26.5 g) were caught on 19 June and confirmed pregnant by palpation of fetuses, and presence of enlarged nipples and vulva (BANWR 2014). In addition, Najera (1994) caught an 8 g juvenile male (age 21- 30 days according to Quimby 1951) on 31 July, that likely would have had been conceived 10 - 19 June (Najera 1994).

Given that there is a lag between conception and ability to detect pregnancy, pregnancies may occur as early as the first week of June at BANWR.

Najera (1994) and Zwank et al. (1997) suspected that breeding at BANWR took place as late as August because they caught young of the year animals in October. However, this ~~interpretation~~ may be incorrect. The size range of jumping mice they caught in October was 15.0 to 24.5 g (mean 18.5 g). These included a 15.5 g female on the last date (22 October) jumping mice were caught. According to Quimby, (1951) this female was approximately 70 days old and hence it had a back-calculated parturition date of 13 August and conception date of 23 July. Thus, no breeding (i.e., conception) is verified after July at BANWR, though some females may not give birth until early August. Similarly, at BANWR males with scrotal testes were captured most frequently in June and July, with a smaller proportion in May; none were found after July (Najera 1994, Wright 2012).

No museum specimens taken at BANWR had data about embryos. A large series of specimens collected at BANWR had been salvaged, apparently drowned, from wading pools that were being used for amphibian experiments in 1977 (D. J. Hafner, in litt.). Those specimens were not used for these analyses because of uncertainty about when each specimen died. Of the remaining specimens, an adult female captured on 22 July and two adult females captured on 2 September were recorded as possessing uterine scars and lactating, suggesting that they had recently or were currently nursing young in a nest.

To summarize reproductive information for BANWR, some males start to become reproductively active in May, with higher proportions becoming reproductively active in June and July (Figure 4). Pregnant females are known from 15 June to 27 July. Other evidence suggests conception during the first and second week of June. There is no convincing evidence for pregnancies in May and no reproductive activity is verified for later than 25 August (Table 4). Independent young first appear in August. However, it should be cautioned that these dates are conservative given the small sample sizes. The earliest verified date of capture for a young of the year is 31 July. Though data are limited, most older adults have immerged into hibernation by the end of the first week in September, with the last young of the year entering hibernation by 26 October.

Reproduction in Other Populations

Information from other valley populations indicates a broader time range for pregnancy as compared with data from BANWR (Figure 4). For instance, data indicate pregnancies can occur in early June. A specimen caught on 13 June from the Rio Grande valley near Isleta was carrying five embryos in an early development stage (< 5 mm long). Similarly, Morrison (1988) caught a 13 g juvenile on 1 August in the Rio Grande valley near Casa Colorada Wildlife Area, Valencia County; assuming it had recently been weaned, the back-calculated conception date was prior to 13 June. Along a western tributary of Sambrito Creek, Archuleta County, Colorado, a 16.5 g juvenile (age class 0.18) male was caught on 25 July; assuming it had recently been weaned, the back-calculated conception date was prior to 6 June. Data also indicate later pregnancy into August. Near Isleta, Valencia County, Morrison (1988) procured a female specimen (age class 0.44) on 19 August that had enlarged mammae and was carrying seven embryos. Based on age class data, young of the year enter the trappable population about 25 July (Figure 3).

Dates for most pregnancies in montane populations are generally later than in valley populations (Figure 4). At Fenton Lake in the Jemez Mountains, Morrison (1987) evaluated males as scrotal between 23 June and 18 July, females as pregnant between 28 July and 15 August, and females having enlarged mammae between 21 July and 29 August. However, in the Jemez Mountains I captured a 22 g female on 1 July that was carrying six 2 mm embryos and a 18.5 g female on 5 July that was carrying six 6 mm embryos. Females specimens with embryos were captured 22 July-16 August (average date 27 July; N = 9) in the White Mountains and 15 July-17 August (average date 26 July; N = 9) in the Sacramento Mountains. Thus, known pregnancies for montane populations ranged from 1 July to 17 August, which are at least 2 weeks later than for BANWR. Based on age class data, young of the year in montane areas enter the trappable population about 17 August (Figure 3).

Bosque del Apache mid-summer activity hiatus

BANWR is the southernmost location for *Z. h. luteus* along the Rio Grande and the lowest elevation location (i.e., highest temperature equivalent) where the species is currently known to persist. Field studies at BANWR have revealed a sharp reduction in detectable above-ground activity of jumping mice during mid-Summer. In 1991 and 1992, Najera (1994) caught jumping mice in June, July, September and October, but caught no jumping mice between 16 July and 10 September, which included a sampling effort of 4,708 trap-nights in August (Najera 1994). In 2009 and 2010, Wright (2012) captured only a juvenile male on 16 August during a 30 July-17 August 2009 trapping period with an effort of 2,910 trap-nights and a 16 g male on 28 August during a 23 August-20 September 2010 trapping period with an effort of 4,320 trap-nights (Table 3).

Part of the reason for the low detectability of jumping mice at BANWR during this time frame (late July to early September) might be because adult males (and possibly non-reproductive adult females) are entering hibernation and adult females are in maternal nests with nursing young quickly followed by immergence into hibernation. However, if all maternal nesting occurred in August we would expect a pulse of young of the year in the trappable population in September. That this happens is suggested by the older specimen data, but not for the more recent field studies (Table 3). Data from Najera (1994) revealed highest relative abundance (captures per 100 trap-nights) of 0.76 in May, which tapered off to 0.32 in June and 0. 24 in July, and with a second minor peak in September (0.08) and October (0.33). In the study by Wright (2012) there was no obvious second peak; relative abundance varied from 0.33 during 12-29 May, 0.42 during 11 June -8 July, 0.27 during 20 July-17 August, 0.02 during 23 August-30 September and 0.05 during 1-25 October. Thus, an additional unknown factor might be occurring to cause this pattern in activity, such as differential trap-avoidance by young animals or an abundance of natural food such as grass seeds that makes trap bait less attractive. Given similarity of climate, it is possible that other populations in the middle Rio Grande and Verde River exhibit the same pattern.

Conclusions

As predicted, *Z. h. luteus* exhibits geographic variation in timing of key life history events, some of which are fundamentally different from other subspecies of *Z. hudsonius* (Figure 4). The duration and timing of the active interval of the population of *Z. h. luteus* at BANWR ~~is~~ most similar to other subspecies of *Z. hudsonius*. The active interval at BANWR was the same as *Z. hudsonius* from Michigan, which has been documented at 162 days (but extended to 165 days in a year of late emergence, Muchlinski 1988). However, the timing differed. Jumping mice at BANWR emerged ca 4 weeks *later* than those in Michigan, which usually emerge in late April (Nichols and Conley 1982, Muchlinski 1988). The timing of emergence in *Z. h. luteus* at BANWR was similar to *Z. h. preblei*, which also occurs in the Rocky Mountains. The mean date of last spring freeze (ca 10 May; The Climate Source 2000) is similar for BANWR, central Michigan, and the Front Range. However, soil temperature regime is a consequence of the radiation regime, moisture content, and snow cover (Baker 1971). Thus, similarities and differences among emergence dates of different species and populations of jumping mice might relate to one of these factors, or to adaptive evolutionary differences.

The greatest deviation from the typical active season pattern of *Z. hudsonius* in the eastern U.S. was observed for montane populations of *Z. h. luteus* (Figure 4). These animals had an active interval reduced by ca 4 weeks (ca 124-135 days) compared with eastern U.S. *Z. hudsonius*. Rather, the active interval was similar to that (124 days) experienced by *Z. princeps* occurring at similar elevations (2,591 m) in Wyoming (Brown 1967). However, again, the timing was different. In part, *Z. princeps* copes with the short summers of high elevation montane sites by hibernating early, with the last individuals captured in early to mid September (earlier at higher elevations). In addition, *Z. princeps* emerges from hibernation 4-8 weeks later than *Z. hudsonius* in the eastern U.S. At the lowest elevations (2,591) *Z. princeps* emerges from hibernation in mid May (16 May), nearly identical to the population of *Z. h. luteus* at BANWR (Brown 1967). However, populations of *Z. princeps* at 2,896 m emerge on 1 June, and those at 3,200 m on 13 June (Brown 1967). Thus, montane populations of *Z. h. luteus* emerge from hibernation as late as very high elevation populations of *Z. princeps*. But, unlike the truncated activity period in fall experienced by *Z. princeps*, young of the year *Z. h. luteus* from montane locations may not enter hibernation until October, like *Z. h. preblei*. Thus, different species and populations of jumping mice adjust to short activity intervals in different ways.

The length of the active interval dictates the maximum duration of reproduction for a population (active interval should not be confused with the above-ground activity period of individuals; adults might have activity periods of < 90 days). There is no evidence for more than one litter per year in *Z. h. luteus*. For montane populations of *Z. h. luteus* there is a single peak in pregnancy in late July. As in *Z. princeps*, which has a similarly short active interval, it seems unlikely that two litters per year are possible for *Z. h. luteus* in montane locations (e.g., Brown 1967, Falk and Millar 1987). To do so, a female would have to conceive the first litter immediately upon emerging from hibernation. She then would have to conceive the second litter while still nursing the first litter. Finally, the young of the second litter would likely have fewer than three weeks following weaning to reach adult size and prepare for hibernation. Such a scenario seems improbable. Data on other jumping mice have shown that younger and lower weight females delay pregnancy, with possibly only females that have achieved their third active season and that emerged from hibernation with excess body weight capable of breeding immediately upon emergence (Brown 1967, Falk and Millar 1987). Cold spring weather conditions can extend the emergence date thereby shortening the active interval. Offspring born later in the season may have relatively lower survival rates due to low body mass, while females that have late litters are likely to have reduced survival due to delayed hibernation and associated energetic costs. Consequently, montane *Z. h. luteus* probably only have a single litter each season.

The situation at BANWR is more complicated. The length of the active interval and timing of reproductive activities in *Z. h. luteus* at BANWR are similar to *Z. h. preblei* (Meaney et al. 2003). In *Z. h. preblei* there are two peaks in reproduction with young of early litters first captured in July, and young of late litters first captured after 1 August; some females might be able to produce two litters ~~(Meaney et al. 2003)~~. Population numbers of *Z. h. preblei* expand in August as a result of young of the year animals entering the population (Meaney et al. 2003). However, field studies on *Z. h. luteus* conducted during the last two decades found no detectable expansion of the population in August, though there is a small pulse of presumably late litter young at the end of the active season (Table 3). Though sample sizes are small, this suggests that there may be little regular production of the crucial early litters at BANWR. ~~Possible explanations include an evolutionary adaptation to avoid early litters or failure to produce early litters due to extrinsic factors.~~

Some possible explanations for extrinsic factors that could reduce reproduction in the BANWR population include lethal genetic abnormalities due to inbreeding depression or reduced opportunity to find mates in this exceptionally small population. However, a more compelling possibility is low body weight of females emerging from hibernation. Periodic arousal from hibernation, which can be caused by warm ambient temperatures, is energetically costly and can deplete fat reserves (French and Forand 2000). Thus, unusually warm or variable temperatures could result in reduced overwinter survival and excessively low body weights in jumping mice upon emergence (Schorr et al. 2009). Ultimately, low body weight in adult females results in lowered reproductive outputs for a population and lowered survival for offspring. Consequently, climate changes that shift phenologies earlier in the spring or that result in increasing depth or duration of warm spells during the winter may cause reduced survival and reproduction in *Z. h. luteus*, especially populations occurring at locations with warmer temperature equivalents. Earlier emergence times could leave metabolically stressed animals in spring without food sources (if the important spring food plants do not also shift to earlier phonologies), while winter warm spells increase potential for arousals that pose metabolic challenge for overwinter survival and subsequent reduced reproduction.

Management Implications

More research is needed on timing of life history events and reproduction in *Z. h. luteus* including populations that represent a range of latitudes and elevations. Special attention should be paid to linkages between overwinter survival and body condition with subsequent reproduction. Compliance surveys, which have the objective of determining presence or absence of *Z. h. luteus* at a project site must occur during times when the population is reliably detectable, if present. I recommend that such surveys occur after all overwintering animals have emerged from hibernation. In addition, surveys conducted in late summer or fall should consider that the adults may enter hibernation in August and that only late litter young of the year are active into fall. Thus, for most populations except the middle Rio Grande, I recommend that compliance surveys are best implemented in July and August. In some cases it might be justifiable to survey montane locations during the last week in June or first two weeks of September, but such surveys might offset lower abundances with larger trap-nights set over more nights. In the middle Rio Grande valley, and possibly other locations with a high relative temperature (Table 2), I recommend that compliance surveys are best implemented from 20 May to 31 July.

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TABLE 1. Percent of records by month for the New Mexico meadow jumping mouse (*Zapus hudsonius luteus*) based on museum specimens from low elevation valleys and montane populations. Percent of records by month for Bosque del Apache National Wildlife Refuge (Valley, Rio Grande population) is based on field data reported by Najera (1994) and Najera et al. (1994).

	Bosque del Apache (N = 78)	Valley (N = 67)	Montane (N = 242)
May	41.0	4.5	0.0
June	28.2	14.9	11.6
July	17.9	29.9	44.2
August	0.0	25.4	30.2
September	3.8	25.4	12.8
October	9.0	0.0	1.2

Table 2. Latitude, elevation, temperature equivalent, and predicted date of first emergence of the New Mexico meadow jumping mouse (*Zapus hudsonius luteus*) from hibernation. The temperature equivalent is a relative measure of mean annual temperature that corrects locations for latitude and elevation according to approximate means in New Mexico and a temperature lag rate of 0.56°C per 1° latitude and 76 m elevation. The predicted date of first emergence is based on the regression equation in Figure 2.

Population	Latitude (degrees)	Elevation (m)	Temperature Equivalent	Predicted date of first emergence	Earliest known dates
Verde River, Camp Verde[a]	34.6	950	66.9	6 May	
Rio Grande, Bosque del Apache	33.8	1,370	62.2	15 May	13 May, 18 May
Rio Grande, Isleta	34.9	1,495	59.5	20 May	24 May
Rio Grande, Espanola	36.0	1,700	55.7	26 May	24 Jun
Sacramento Mountains, Tularosa Creek	33.1	2,050	54.0	29 May	18 June
White Mountains, Campbell Blue Creek	33.7	2,000	54.1	29 May	
Sacramento Mountains, Rio Penasco	32.8	2,170	52.7	1 June	
Piedra River, Sambrito Creek	37.0	1,860	52.6	1 June	28 May[b]
Florida River, Florida	37.2	2,050	49.9	6 June	
White Mountains, West Fork Black River	33.8	2,330	49.6	6 June	20 June
Mora River, Mora	36.0	2,185	49.3	7 June	
Sangre de Cristo Mountains, Fort Burgwin	36.3	2,250	48.2	9 June	
Jemez Mountains, Fenton Lake	35.9	2,350	47.3	10 June	13 June
White Mountains, North Fork White River	34.0	2,500	47.2	11 June	24 June

Jemez Mountains, San Antonio Creek	35.9	2,355	47.2	11 June	28 June
Sacramento Mountains, Aqua Chiquita Creek	32.7	2,600	47.2	11 June	
Sangre de Cristo Mountains, Sugarite Canyon	37.0	2,300	46.8	11 June	11 June
Sangre de Cristo Mountains, Coyote Creek	36.2	2,365	46.8	11 June	
Sacramento Mountains, Mauldin Spring	36.8	2,680	46.0	13 June	
Sangre de Cristo Mountains, Rito la Presa[c]	36.1	2670	42.9	18 June	
White Mountains, Lee Valley Creek	33.9	2,880	42.3	19 June	
Sangre de Cristo Mountains, Rio Hondo[c,d]	36.6	2870	39.7	24 June	

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[a] See Frey (2012) for information about a population in the Verde River watershed.

[b] Personal communication J. L. Zahratka.

[c] See Frey (2008) for information about this location.

[d] See Hafner et al. (1981) and Frey (2008) and for information about this population.

TABLE 3. Age of New Mexico meadow jumping mice (*Zapus hudsonius luteus*) by month captured in the middle Rio Grande valley at Bosque del Apache National Wildlife Refuge, Socorro County, New Mexico. The number of known pregnant females is indicated with a "p" in parentheses.

	Museum specimens[a]			Najera (1994); Najera et al. (1994)[b,d]		Wright (2012); Frey and Wright (2012)[c,d]	
Month	Juvenile	Subadult	Adult	Young of Year	Adult	Young of Year	Adult
May	0	0	0	0	34	0	10
June	0	0	4	0	26 (p=1)	0	7 (p=1)
July	0	2	3	1[e]	14 (p=5)	0	11 (p=6)
August	1	10	0	0	0	2[f]	0
September	2	8	2	1	2	0	0
October	0	0	0	7	0	1	0

[a] All museum specimens were collected 1976-1979. Fifteen of the specimens were found drowned in wading pools that had been set up for a toad behavioral study in 1977-1978 (D.J. Hafner in litt.). Hence, recorded dates might be later than actual date of death. Aging of specimens was via cranial and dental characters as described in the text.

[b] Results are combined for data collected June-October 1991 and May-July 1992.

[c] Results are combined for May-August 2009 and May-October 2010.

[d] Following Nichols and Conley (1982) and Meaney et al. (2003) all May and June individuals were assumed to be adults (i.e., overwintered), regardless of body mass. For July, it was assumed that independent young could first appear on 11 July (based on average date of female emergence plus 49 days for gestation and nursing) at which time they weigh ca 8-10 g. I regarded any animal < 14 g (i.e., lowest known weight of an adult in spring) in July as young of the year. For August - October, I used the relation illustrated by Meaney et al. (2003) between date and body mass of *Zapus hudsonius preblei* to distinguish age classes.

[e] An 8g juvenile male caught on 31 July.

[f] A 7g juvenile male caught on 16 August and a 16 g male caught on 28 August; the 16 g male was considered young of the year based on Meaney et al (2003).

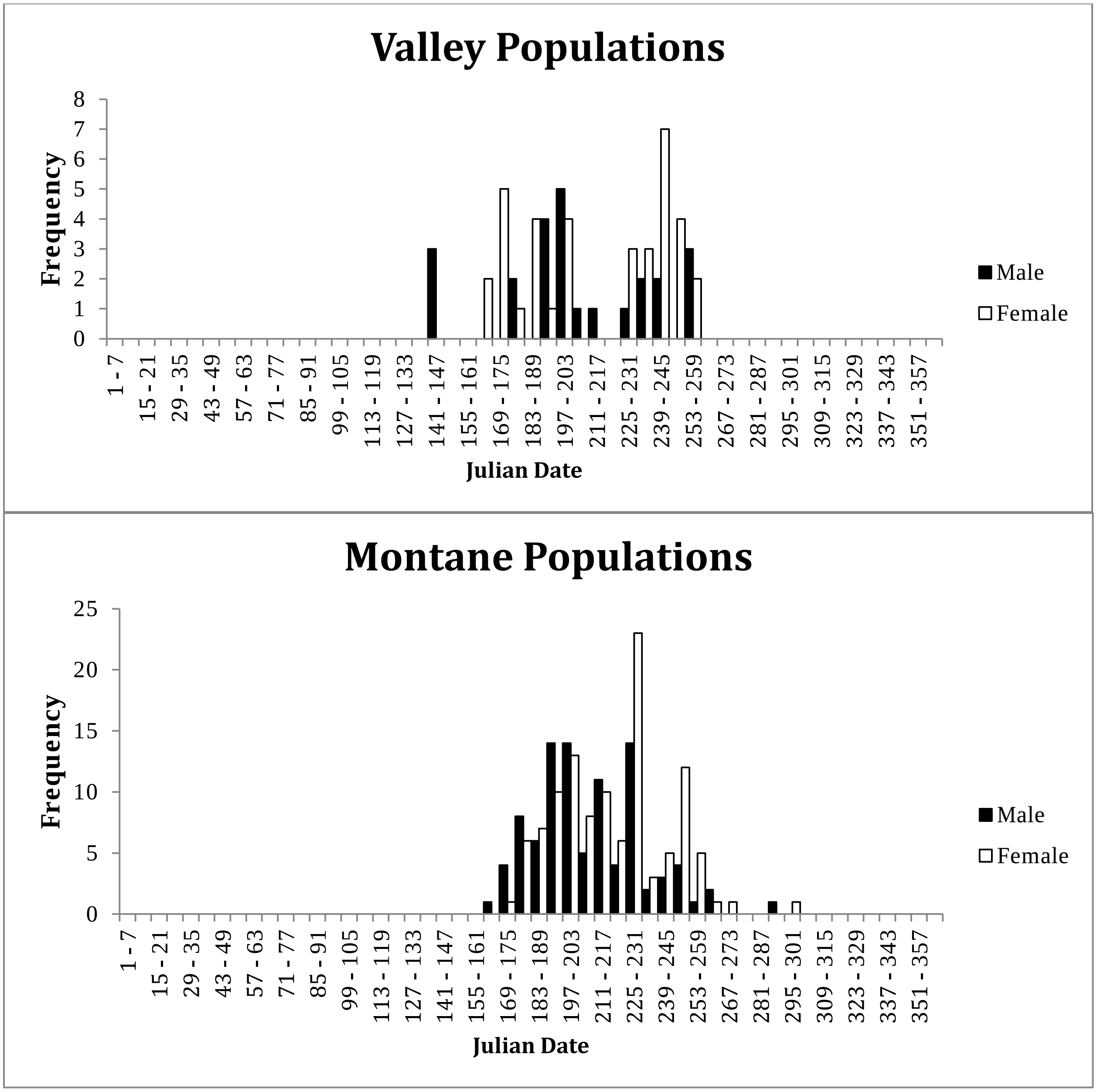

Figure 1. Activity season of male (black bars) and female (white bars) New Mexico meadow jumping mice (*Zapus hudsonius luteus*) from valley (top) and montane (bottom) populations based on dates of capture recorded on museum specimen labels. Julian date equivalents are 121 = 1 May, 152 = 1 June, 182 = 1 July, 213 = 1 August, 244 = 1 September, 274 = 1 October, 305 = 1 November.

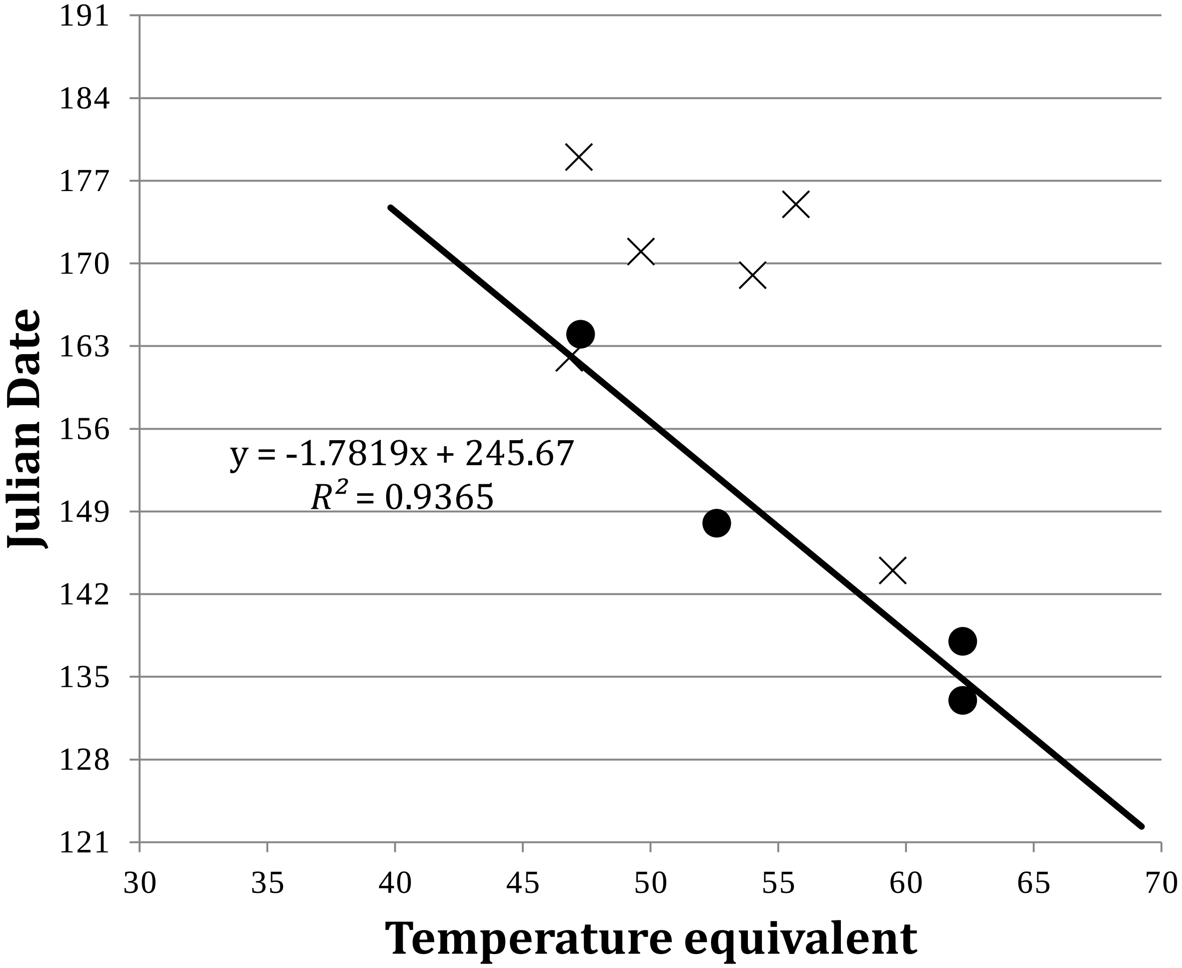

Figure 2. Relationship between the temperature equivalent of a location and the earliest known date for emergence of the New Mexico meadow jumping mouse (*Zapus hudsonius luteus*) from hibernation. Solid dots and regression line are based on dates of earliest capture during field studies; X's are earliest dates of representative museum specimens. Julian dates range from 1 May (121) to 10 July (191).

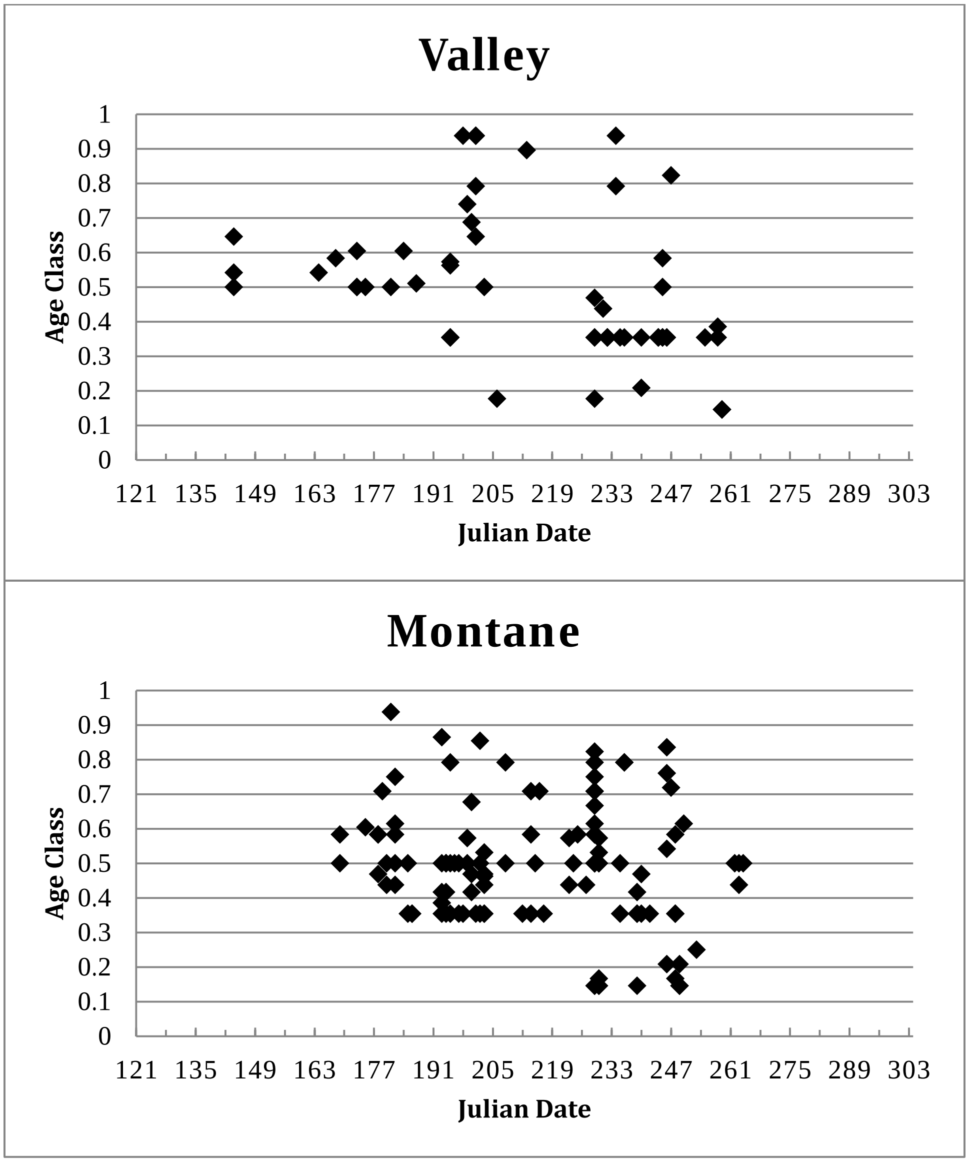

Figure 3. Age class of specimens of the New Mexico meadow jumping mice (*Zapus hudsonius luteus*) by date of capture for valley (top) and montane) populations. Age class was determined by characteristics of the skull and dentition.

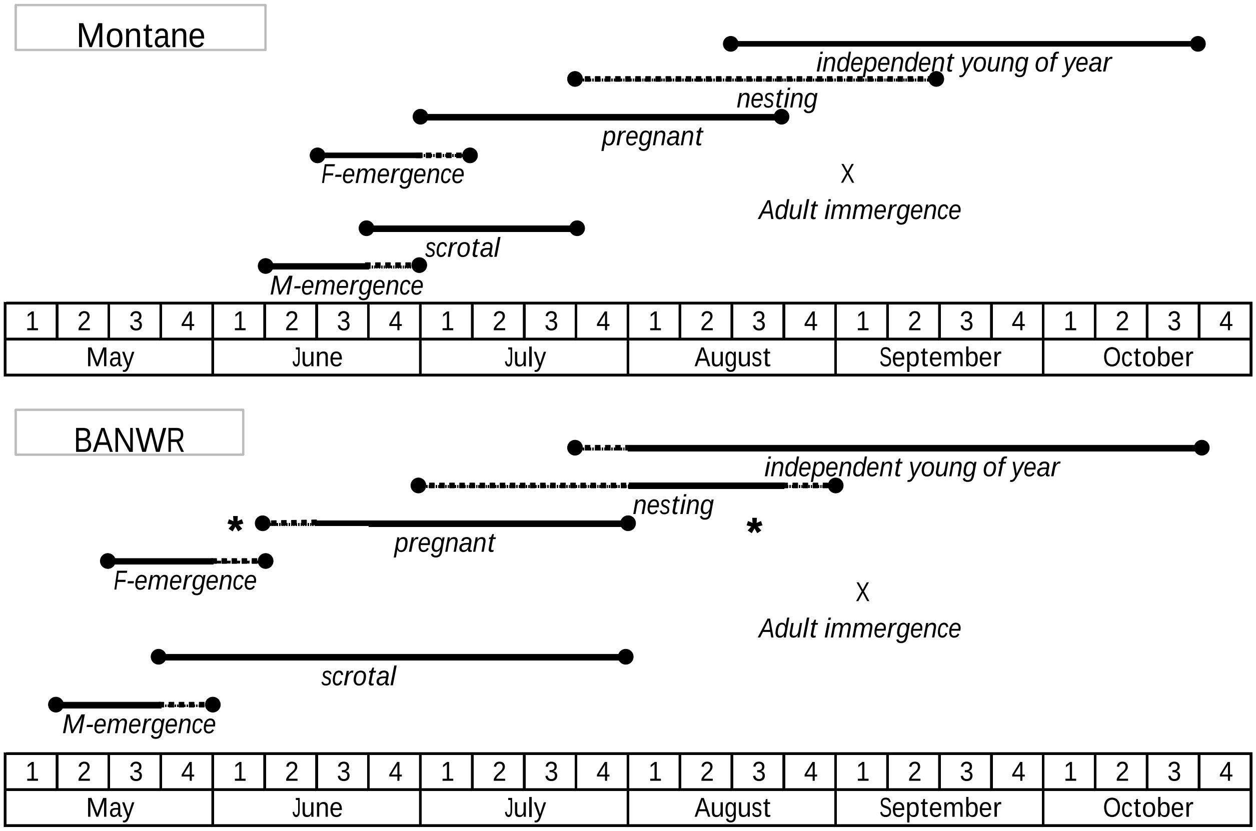

Figure 4. Generalized schematic of the timing of key life history events for the New Mexico meadow jumping mice (*Zapus hudsonius luteus*) in montane populations (top) and a low elevation valley site at Bosque del Apache National Wildlife Refuge (BANWR; bottom). Solid lines represent time frames documented by evidence; dashed lines represent time frames inferred from other evidence. Asterisks indicate pregnant females captured at other valley locations (Sambrito Creek and Isleta) that suggest a wider possible time frame for pregnancies at BANWR.