Variation in phenology of hibernation and reproduction in the endangered New Mexico meadow jumping mouse (Zapus hudsonius luteus)

Jennifer Frey

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 lower elevation valley populations. A low-elevation population located at Bosque del Apache National Wildlife Refuge (BANWR) in the Rio Grande valley was most similar to other subspecies 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 124-135 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). In montane populations pregnant females are known from July to late August and evidence suggests that they have a single litter per year. At BANWR two peaks in reproduction were expected based on similarity of active season to *Z. h. preblei*. However, only one peak was clearly evident, possibly due to later first reproduction and possible torpor during late summer. At BANWR pregnant females are known from June and July. Due to the short activity season and geographic variation in phenology of key life history events of *Z. h. luteus*, recommendations are made for the appropriate timing for surveys for this endangered species.

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2 **Mexico meadow jumping mouse (*Zapus hudsonius luteus*)**

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8 ## Abstract

9 Hibernation is a key life history feature that can impact many other crucial aspects of a species'
10 biology, such as its survival and reproduction. I examined the timing of hibernation and
11 reproduction in the federally endangered New Mexico meadow jumping mouse (*Zapus hudsonius*
12 *luteus*), which occurs across a broad range of latitudes and elevations in the American Southwest.
13 Data from museum specimens and field studies supported predictions for later emergence and
14 shorter active intervals in montane populations relative to lower elevation valley populations. A
15 low-elevation population located at Bosque del Apache National Wildlife Refuge (BANWR) in the
16 Rio Grande valley was most similar to other subspecies of *Z. hudsonius*: the first emergence date
17 was in mid-May and there was an active interval of 162 days. In montane populations of *Z. h. luteus*,
18 the date of first emergence was delayed until mid-June and the active interval was reduced to ca
19 124-135 days, similar to some populations of the western jumping mouse (*Z. princeps*). Last date of
20 immergence into hibernation occurred at about the same time in all populations (mid to late
21 October). In montane populations pregnant females are known from July to late August and
22 evidence suggests that they have a single litter per year. At BANWR two peaks in reproduction
23 were expected based on similarity of active season to *Z. h. preblei*. However, only one peak was
24 clearly evident, possibly due to later first reproduction and possible torpor during late summer. At
25 BANWR pregnant females are known from June and July. Due to the short activity season and
26 geographic variation in phenology of key life history events of *Z. h. luteus,* recommendations are
27 made for the appropriate timing for surveys for this endangered species.

Introduction

Hibernation is an adaptive strategy that some mammals use to cope with long-term seasonal limitations in food or water (Davis 1976, Heldmaier et al. 2004, Ruf and Geiser 2014). Hibernation is characterized by prolonged multiday bouts of torpor during which the animal's metabolic rate is significantly lowered, body temperature decreases toward ambient temperature, and many physiological functions cease (Williams et al. 2011, Ruf and Geiser 2014). Thus, while hibernation can confer profound savings of water and energy, and it has other indirect benefits such as increased survival through predator avoidance, it also bears costs related to altered physiological functions and reduced opportunity for reproduction (Ruf and Geiser 2014). Despite a great deal of research on the physiology of hibernation, there has been disproportionately little research on the ecological consequences of hibernation (Lane 2012). Elucidating the timing and duration of biological events associated with hibernation is central to understanding its ecological consequences, because hibernation is tightly linked to other crucial aspects of a species' biology (Kirkland and Kirkland 1979, Turbill et al. 2011). Recovery from hibernation, reproduction, and sequestering energy reserves to enter and survive the next hibernation all must happen within a brief active period during the warmer months. Thus, 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 (e.g., Muchlinski 1988, Dobson et al 1992, Ozgul et al. 2010, Sheriff et al 2011). Thus, understanding the phenology of hibernation and reproduction is central to understanding the life history of hibernating species. Such questions have gained increased importance due to the potential for altered phenology and mismatches in the phenology of interacting species as a consequence of climate change (e.g., Inouye et al 2000, Lane 2012, Boutin and Lane 2013, Sheriff et al 2011, 2013).

Most studies on variation in phenology of the annual cycle of mammalian hibernators have been conducted on ground squirrels (Sciuridae: Marmotini) and dormice (Gliridae). The jumping mice (Dipodidae: Zapodinae) are another group of small mammal hibernators that are confronted with strongly seasonal environments in the northern temperate zone. However, there has been comparatively little research on hibernation in jumping mice, especially with respect to variation in phenology of the annual cycle (e.g., Lyman et al 1982). In comparison with most ground squirrels and dormice, jumping mice have much smaller body size (< 25 g) and they have not been reported to cache food (Vander Wall 1990). Although terrestrial mammal hibernators usually are small, in part to facilitate use of underground burrows that are buffered from thermal extremes, hibernators benefit from relatively large body size (while still remaining small enough to burrow) because the principle source of energy for most hibernators during torpor is body fat (Humphries et al. 2003, Florant and Healy 2012). However, many granivorous hibernators also utilized cached seeds for food during the hibernation period, which allows greater flexibility in use of torpor (e.g., Vander Wall 1990, French 2000, Humphries et al. 2003, Sheriff et al 2011). Jumping mice are somewhat unique among granivores in that they apparently do not use food caches and hence must rely on body fat for all energy needs during hibernation (French 1985, Humphries et al. 2003). Thus, the phenology of the annual cycle in jumping mice, with its attendant costs and benefits, may differ in comparison with other taxonomic groups.

71   Other than through use of radio-telemetry, there are no effective methods to detect most
72   species while they are in hibernation, since they are inactive in underground burrows.
73   Consequently, in order to study these animals in the wild, information must be available on when
74   they are active above ground. This is particularly true for threatened and endangered species
75   because populations must be monitored to detect trends, and surveys for the species presence are
76   often required in areas of potential habitat when activities might cause harm to the animals if
77   present. For instance, the New Mexico meadow jumping mouse, *Zapus hudsonius luteus*, was listed
78   as endangered under the U.S. Endangered Species Act in June 2014 due to substantial declines in
79   populations over the last several decades (USFWS 2014). This subspecies was originally described
80   as a distinct species (Miller 1911) and recent molecular analyses have validated it as relatively
81   diverged monophyletic clade (Malaney and Cook 2013). *Zapus h. luteus* occurs in the American
82   Southwest, with an historical range that included portions of southern Colorado, New Mexico, and
83   central and eastern Arizona (Hafner et al. 1981, Frey 2012, Malaney et al. 2012). It is a specialist of
84   riparian habitats and hence its distribution includes both low elevation sites within desert biomes
85   and high elevation sites within boreal biomes (Frey and Malaney 2009, Malaney et al. 2012).

86   The known distribution of *Z. h. luteus* extends between 32.7° N and 37.2° N latitude and
87   between 1,375 m and 2,926 m elevation, possibly as low as 935 m (i.e., Camp Verde, Yavapai
88   County, Arizona; Frey 2008, 2012). Given the large size and extreme topographic variability of this
89   region, *Z. h. luteus* is expected to exhibit geographic variation in phenology of its hibernation and
90   reproduction. However, there is little existing information on phenology of the annual cycle in this
91   taxon. In addition, there are relative few studies on phenology of the annual cycle in other taxa of
92   jumping mice. Within other subspecies of the meadow jumping mouse, *Z. hudsonius*, phenology has
93   been described at four locations, three in the eastern U.S. (Minnesota, Quimby 1951; New York,
94   Whitaker 1963; Michigan, Nichols and Conley 1982, Muchlinski 1988;) and one in Colorado
95   (Meaney et al. 2003), but none of these studies evaluated variation in phenology at locations in
96   different environments. Within the western jumping mouse, *Z. princeps*, phenology has been
97   described for a population in Alberta (Falk and Miller 1987), and three studies have evaluated
98   variation in phenology of different populations living in different environments in Wyoming
99   (Brown 1967) and Utah (Cranford 1978, 1983). No studies have evaluated phenology of
100 hibernation in the Pacific jumping mouse, *Z. trinotatus* (Verts and Carraway 1998).   A comparison
101 of these studies indicates that different species and populations of jumping mice exhibit different
102 phenologies, rendering inference to *Z. h. luteus* impossible. Thus, the purpose of my study was to
103 determine the timing of hibernation and reproduction in *Z. h. luteus* and to compare the phenology
104 with other taxa of jumping mice. First, although the annual cycle for most hibernators is similar, I
105 summarize existing knowledge about the phenology of hibernation and reproduction in jumping
106 mice, with a specific focus on *Z. hudsonius*, in order to establish specific assumptions to be tested.

107 **Hibernation and reproductive phenology in jumping mice**

108   Jumping mice (Subfamily Zapodinae) are in the Holarctic rodent Family Dipodidae, which
109 also includes the birchmice (subfamily Sicistinae) and jerboas (subfamilies Allactaginae,
110 Cardiocraniinae, and Dipodinae). Traditionally, Zapodinae includes five species: the Chinese
111 jumping mouse (*Eozapus setchuanus*), and two genera endemic to North America, including the

112 woodland jumping mouse (*Napaeozapus insignis*), and three species of jumping mice (genus *Zapus*;
113 Wilson and Reeder 2005). The genus *Zapus* (hence forth, jumping mice) have a boreo-montane
114 distribution. The meadow jumping mouse (*Z. hudsonius*) has the largest geographic range, which
115 extends across the boreal zone of Alaska and Canada and in the eastern U.S. south through the
116 southern Appalachian Mountains region (Laerm et al. 1996). *Z. hudsonius* also occurs as isolated or
117 semi-isolated populations in the western U.S., including along the east slope of the Front Range of
118 the Rocky Mountains (*Z. h. preblei*) and in the American Southwest (*Z. h. luteus*; Malaney et al.
119 2012). The western jumping mouse (*Z. princeps*) occurs throughout the Rocky Mountain region,
120 from southern Alaska south into the Sierra Nevada of California and the Southern Rocky Mountains
121 in northern New Mexico, with an eastern extension across the northern Great Plains to Minnesota
122 (Malaney et al. 2013). However, recent phylogenetic analyses indicate *Z. princeps* is represented by
123 at least 5 clades, which may redefine species boundaries (Malaney et al. 2013). Lastly, the Pacific
124 jumping mouse (*Z. trinotatus*) is restricted to the Sierra Nevada and Pacific coastal area from
125 southern Canada south into California (Wilson and Reeder 2005). Malaney et al. (2013) found that
126 *Z. princeps* is paraphyletic with respect to *Z. trinotatus*, but no taxonomic conclusions were made.

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

142   Evidence suggests that photoperiod cues immergence into hibernation by *Z. hudsonius* in
143 the eastern U.S. (Neumann and Cade 1964, Muchlinski 1978, 1980b). Because timing of
144 immergence is cued by photoperiod, entrance into hibernation by adult *Z. hudsonius* may be more
145 uniform both geographically and annually, in comparison to emergence. Hibernation is preceded
146 by a critical ca 2 week period of rapid weight gain (e.g., 8% per day; Quimby 1951, Morrison and
147 Ryser 1962, Muchlinski 1988). In the eastern U.S., adults undergo weight gain during late August
148 and all have entered hibernation by about the end of the first week in September (Muchlinski
149 1988). Adult males enter hibernation first, followed by adult females; juveniles enter hibernation
150 last with timing dependent on birth date (later litters entering hibernation as late as October;
151 Muchlinski 1988). In contrast, immergence in *Z. princeps* was thought to be cued by availability of
152 seeds in the diet rather than photoperiod (Cranford 1978). This difference may be a strategy that
153 allows *Z. princeps* to cope with a much shorter period of above ground activity in the high elevation

154   sites it occupies (i.e., ca 2.7 - 4 months as compared with ca 5.5 months in many eastern U.S.
155   populations of *Z. hudsonius*; Cranford 1978, 1983, Muchlinski 1980b). During years with late spring
156   emergence and plant growth, there might not be enough time for jumping mice to accumulate fat
157   reserves if immergence was consistently cued by day length. Consequently, cueing on availability of
158   seeds is thought to allow *Z. princeps* to initiate hibernation when conditions are most favorable
159   (Muchlinski 1980b).

160   One of the main constraints of a short activity season is the number of litters that can be
161   produced annually. Mating apparently occurs soon after the females have emerged from
162   hibernation (Whitaker 1972) and hence timing of spring emergence influences the time available
163   for females to raise young to weaning and then for young of the year to mature and ultimately gain
164   fat in preparation for hibernation. Variation in emergence times in *Z. hudsonius* has resulted in
165   litters being produced 2-3 weeks later in some years (Muchlinski 1988). Gestation is 18-21 days
166   (Quimby 1951) and it then requires ca 4 weeks after birth before the young are weaned and
167   become independent (Whitaker 1972). It required ca 90 days for a juvenile jumping mouse to
168   attain a mass of 20 g, which is adult size (Quimby 1951). Preparation for hibernation then requires
169   a 2-week period of fattening (Morrison and Ryser 1962). Thus, the minimum time required from
170   conception to hibernation in *Z. hudsonius* is ca 125 days. In *Z. hudsonius* from the eastern U.S. the
171   active interval, which is the number of days from emergence of the first animal in the spring to the
172   immergence of the last animal in fall, is 162-165 days (Muchlinski 1988). Evidence suggests that
173   female *Z. hudsonius* must achieve a large body mass in order to reproduce, which can result in
174   delays in reproduction (Falk and Miller 1987). Thus, some females produce their first litter within
175   a month after emergence (i.e., early breeding females), while females that did not breed during the
176   first month may produce a litter during the second month after emergence (i.e., late breeding
177   females; Quimby 1951). In the eastern U.S., both early and late breeding females may produce a
178   second litter, young of early litters may breed, and there is some evidence that lactating females can
179   become pregnant (Quimby 1951; Nichols and Conley, 1982). Hence, in the eastern U.S. there are
180   two (sometimes three) peaks in reproduction during the active season and individual females may
181   produce two and conceivably three litters per year (Quimby 1951, Whitaker 1963, Nichols and
182   Conley 1982). Similarly, both early and late litters were detectable in *Z. h. preblei*, even though it
183   has a shorter active season (150 days; Meaney et al. 2003). In *Z. princeps*, females that emerge from
184   hibernation with low body weights (i.e., young of prior breeding season) are more likely to delay
185   reproduction and have smaller litters (Brown 1967, Falk and Millar 1987). Compared to other
186   demographic groups, young of late litters must extend their activity season later into the fall in
187   order to gain weight; even so, these young ultimately have lower survival likely due to a longer
188   period of exposure to predators and lower body weights when entering hibernation (Muchlinski
189   1988, Meaney et al. 2003, Schorr et al. 2009).

190   On basis of observed patterns in phenology of hibernation and reproduction in other
191   jumping mice, I expected for *Z. h. luteus* that: 1) emergence from hibernation in spring will be later
192   for higher latitudes and higher elevations due to overall cooler climate and hence cooler soil
193   temperatures; 2) immergence into hibernation will be later for lower latitudes and lower elevations
194   due to longer growing seasons; 3) the active interval will be shorter for montane populations as
195   opposed to valley populations, and 4) the number of litters possible will be reduced for montane

196 populations. I also report an apparent midsummer hiatus in above ground activity by *Z. h. luteus* at
197 Bosque del Apache National Wildlife Refuge (BANWR), which is the lowest elevation and warmest
198 site known to be currently occupied by the taxon.

199 ## Methods
200   Currently, field studies to examine phenology of the few remaining populations of *Z. h.*
201 *luteus* are not generally feasible because such studies require trapping animals and the populations
202 are small and at high risk of extinction (USFWS 2014). Consequently, I extracted data from
203 museum specimens to supplement the limited information available in published literature (Zwank
204 et al. 1997, Wright and Frey 2015), unpublished theses (Najera 1994, Wright 2012), and agency
205 reports (Morrison 1987, 1988, Najera et al. 1994, Wright and Frey 2010, Frey and Wright 2012,
206 BANWR 2014). This included all known specimens of *Z. h. luteus* with recorded dates of capture (N
207 = 309) and represented the taxon's current geographic range (Supplemental Table 1). Specimens
208 were captured by me (N = 63) or were in the following museum collections: Academy of Natural
209 Sciences of Philadelphia (ANSP; N = 10); Arizona State University Mammal Collection (ASUMC; N =
210 6); Denver Museum of Natural History (DMNH; N= 14); University of Kansas, Museum of Natural
211 History (KU; N=5); Museum of Northern Arizona (MNA; N = 7); University of New Mexico, Museum
212 of Southwestern Biology (MSB; N = 118); University California, Berkeley, Museum of Vertebrate
213 Zoology (MVZ; N = 11); New Mexico Museum of Natural History and Science (NMMNHS; N = 2);
214 New Mexico State University, Vertebrate Collection (NMSU; N = 6); San Diego Natural History
215 Museum (SDNHM; N = 25); Museum of Texas Tech University (TTU; N = 1); University of Arizona,
216 Collection of Mammals (UA; N = 9); University of Illinois Museum of Natural History (UIMNH
217 [collection transferred to MSB]; N = 6); University of Utah, Utah Museum of Natural History (UMNH;
218 N = 7); United States National Museum (USNM; N = 18); Western New Mexico University (WNMU; N
219 = 1).

220   Because soil temperature is influenced by elevation and latitude, I categorized specimens
221 into nine populations divided into two groups: montane (N = 242; Sangre de Cristo Mountains,
222 Jemez Mountains, Sacramento Mountains, White Mountains) and valley (N = 67; Florida River,
223 Sambrito Creek, Mora River, Rio Chama, Rio Grande). I constructed histograms of numbers of
224 specimens of each sex by Julian date to evaluate times of emergence from and immergence into
225 hibernation. The Julian date represents the day a specimen was captured. Because trapping does
226 not necessarily detect either the first or last above ground activity of a population, dates of
227 emergence and immergence should be considered conservative estimates. I examined timing of
228 emergence according to relative temperature equivalents of locations. To a large extent, the climate
229 of a location is ultimately based on its latitude and elevation (i.e., higher latitudes and higher
230 elevations have cooler temperatures). Consequently in order to compare locations that vary in
231 latitude and elevation I calculated a temperature equivalent for locations based on the method
232 described in Frey et al. (2007). The temperature equivalent was set in relation to a hypothetical
233 location located 34° N latitude, 1,981 m elevation with a mean annual temperature of 12.2°C, which
234 are approximate averages for New Mexico. The temperature lapse rate was set to 0.56°C per 1°
235 latitude and per 76.2 m elevation. The temperature equivalent (in Celsius) for a location was

236   calculated: TE = 12.2 + ([1,981 – elevation in meters]*[0.556/76.2]) + ([34 – degrees
237   latitude]*0.556).

238   For museum specimens, I examined cranial and dental characters when possible to
239   establish relative age. Specimens were assigned to 1 of 6 age classes according to wear on the
240   cheekteeth as described by Krutzsch (1954) and specimens were assigned to 1 of 8 age classes
241   based on eruption and wear on the third upper molar (M3) and closure of the basioccipital-
242   basisphenoid suture according to Jones (1981). The Krutzsch (1954) and Jones (1981) age classes
243   for a specimen were transformed into fractions of the total age class possible (e.g., a Krutzsch age
244   class 4 = 4/6 = 0.66). Following Frey (2008), the age class was the mean of the two fractions for an
245   individual. No studies have correlated age classes based on cranial and dental features with known
246   age individuals. Consequently, based on an examination of age classes of animals by date of capture
247   (Figure 1), I distinguished between two age groups: young of the year and adult. All animals
248   immerging from hibernation were at age class $\geq$ 0.35. During hibernation growth essentially ceases
249   and no wear on teeth occurs because jumping mice are not eating. Consequently, I considered age
250   class 0.35 to include both older young of the year animals entering hibernation at the end of their
251   first growing season, and adults emerging from hibernation during their second active season (i.e.,
252   first breeding season). I considered animals at age class > 0.35 to be older, but of unknown age.
253   Animals in age class < 0.35 were considered young of the year, with animals in age class ca 0.2
254   considered recently weaned juveniles.

255   For museum specimens, the primary data I used to establish timing of reproduction was
256   evidence of pregnancy via counts of embryos recorded on specimen tags because these data are
257   unequivocal. I did not consider specimen tag data on lactation reliable because "lac" may be
258   recorded for females in a variety of conditions such as swollen mammae or post-lactation. I used
259   specimen data on reproductive condition of males only to supplement the pregnancy data because
260   data on scrotal versus nonscrotal testes were sparse. I used a 21-day gestation period (though
261   gestation actually may vary from 18-21 days), a 28-day nesting period (time from parturition to
262   weaning and independence), and growth rates for young of the year animals to back-calculate dates
263   of conception and parturition, though it is cautioned that back-calculated dates based on mass of
264   juveniles are often overestimated (Quimby 1951).

265   **Problems identifying reproductive state during field studies**

266   I found inconsistencies in the recording of pregnancy in field data. Najera (1994) and
267   Wright (2012) reported jumping mice of all ages, including juveniles and pregnant females, during
268   May at BANWR. However, evidence suggests that some assignments of age and reproductive status
269   were incorrect. First, while some field studies of jumping mice have used body mass as an indicator
270   of age (e.g., Brown 1967, Nichols and Conley 1982), body mass is highly variable within individual
271   jumping mice and overwintered adults can emerge from hibernation with relatively low body mass
272   (< 20 g; Quimby 1951, Meaney et al. 2003). As an example, Wright (2012) captured a jumping
273   mouse that was unequivocally a juvenile (7 g and juvenile pelage) on 16 August 2009. This animal
274   was recaptured the following spring on 18 May 2010, at which time it weighed only 14 g, which
275   equates to a 60 day old juvenile (Quimby 1951)! Hence, body weight alone cannot be used to
276   determine age, at least in the early part of the active season (Meaney et al. 2003).

277   Second, evidence suggests that some field evaluations of pregnancy may be inaccurate. For
278   instance, Wright (2012) reported capturing 9 females that were evaluated as pregnant
279   (Supplemental Table 2). Of those, 7 had excessive body weight (> 22 g; Meaney et al. 2003) or
280   enlarged mammae that corroborated pregnancy. In addition, 7 were radio-tracked. Three
281   exhibited normal activity behaviors during the radio-tracking session, which consisted of nightly
282   foraging in herbaceous wetland habitats and nesting during the day in above-ground nests in
283   grasses (Wright and Frey 2015). In contrast, four exhibited dramatically different behaviors that
284   were interpreted as tending a maternal nest with nursing young, although the possibility that these
285   females had entered hibernation cannot be discounted. These females left their typical wetland
286   habitats and became almost entirely inactive for ca 2 or more weeks in underground burrows
287   located in woody habitats devoid of herbaceous vegetation. Ryon (2001) described a similar
288   burrow that was used as a maternal nest by *Z. h. preblei*. Importantly, no females captured in May
289   and recorded as pregnant had corroborating evidence of pregnancy. Therefore, it is possible that
290   fat layers remaining from hibernation made the females appear pregnant when they were not.
291   Consequently, field evaluations of pregnancy should be suspect without corroborating information
292   such as swollen mammae, palpated fetuses, excessive weight, or behavioral changes. Thus, for field
293   data I only considered females as pregnant if they were recorded as pregnant and there was some
294   other data corroborating pregnancy such as excessive body mass (> 22 g), which is consistent with
295   late pregnancy (Quimby 1951, Meaney et al. 2003).

296   ## Results

297   **Emergence from hibernation**

298   Emergence from hibernation was earlier for some valley populations than montane
299   populations (Figure 2). The earliest captures represented by the specimens were 3 males on 24
300   May from the Rio Grande valley population (Isleta Pueblo; 34.9° N latitude, 1,495 m elevation).
301   However, field studies recorded slightly earlier dates. Further south along the Rio Grande at
302   Bosque del Apache National Wildlife Refuge, Socorro County (BANWR; 33.8° N latitude, 1,370 m
303   elevation), Najera (1994; see also Zwank et al. 1997) trapped for *Z. h. luteus* beginning in March
304   1992, but did not capture a jumping mouse until 13 May. Males made up 83% of captures during
305   May with the first female caught on 20 May (Najera 1994). The report of a capture on 13 March by
306   Zwank et al. (1997) is an error (see Table 15 and Appendix B in Najera 1994). During another
307   study at BANWR during 2009 - 2011, trapping started on 13 May with the first captures (two
308   males) on 18 May 2010; the first female that year was not caught until 18 June (Wright 2012, Frey
309   and Wright 2012). During the previous year, trapping started 21 May with a male caught on 22
310   May and the first female caught on 26 May; over both years 78% (N = 9) of jumping mice caught in
311   May were male. The earliest capture date for a valley specimen outside the middle Rio Grande
312   valley were two females caught 24 June at Espanola, Rio Arriba County, New Mexico (36.0°N
313   latitude, 1,700 m elevation).

314   No specimens from montane areas have been captured in May (Table 1). The earliest
315   capture represented by specimens from montane areas was a male caught 11 June at Sugarite
316   Canyon, Las Animas County, Colorado (37.0°N latitude, 2,300 m elevation; Jones 1999). Earliest

317   dates of specimens in other well-sampled montane populations include 18 June (Sacramento
318   Mountains: Tularosa Creek, Otero County, 33.1°N latitude, 2,050 m elevation), 20 June (White
319   Mountains: West Fork Black River, 33.8°N latitude, 2,330 m elevation), and 28 June (Jemez
320   Mountains: San Antonio Creek, Sandoval County, 35.9°N latitude, 2,355 m elevation). Of 12
321   montane specimens with June capture dates and gender data, only 4 were females, which were
322   taken 18, 27, 29, and 30 June. Morrison (1987) conducted the only field study that attempted to
323   determine timing of emergence in a montane population at Fenton Lake in the Jemez Mountains,
324   Sandoval County, New Mexico (35.9° N latitude, 2,350 m elevation). Her first capture was a male on
325   13 June with the first female not captured until 27 June (Morrison 1987). She caught a total of 14
326   males and 1 female during June (Morrison 1987).

327   The relationship between temperature equivalents of locations and known first emergence
328   dates predicted that for each degree Celsius increase in temperature equivalent the emergence date
329   would occur more than three days earlier (Figure 3). Dates of earliest known museum specimens
330   from specific locations often were later than predicted, likely due to small sample sizes and because
331   specimens were collected incidentally without special attempt to determine emergence date.
332   Predicted dates of *first* emergence for key populations of *Z. h. luteus* extend over 47 days from 6
333   May to 22 June (Table 2). It should be noted that variation will exist around these predicted dates
334   due to small sample sizes, coarse nature of the model, and annual and site-specific variation in soil
335   temperature.

336   To summarize available information on emergence dates for *Z. h. luteus*, valley populations
337   emerge from hibernation in mid-May, with the earliest above-ground activity recorded on 13 May
338   at BANWR. This early date of emergence is fairly reliable because trapping had started earlier in an
339   attempt to determine emergence. The only similar field study in a montane population (Fenton
340   Lake) documented the earliest above-ground activity on 13 June. In other montane populations,
341   dates of capture for museum specimens were as early as 11 June at Sugarite Canyon. Although
342   details about trapping dates are not available for the Sugarite Canyon example, I consider this date
343   fairly accurate because trapping began in May and the 11 June date was represented by the capture
344   of two nonscrotal males (Jones 2002). In both valley and montane populations, males emerge from
345   hibernation first; males make up the majority of captures during May and June, for valley and
346   montane populations respectively.

Immergence into hibernation

348   Among specimens from low elevation valley populations, none had capture dates after 16
349   September (Table 1, Figure 2). Data on age class revealed that older adult age classes disappeared
350   by 4 September, while younger animals disappeared by 16 September (Figure 1). However, field
351   studies reveal later dates of immergence. During a 7 – 19 September trapping period in the Rio
352   Chama and Rio Grande valleys near Espanola, Rio Arriba County, Morrison (1988) caught two
353   males with weights (31.5 g and 37.0 g) that are typical of adult jumping mice imminently ready to
354   enter hibernation.

355   At BANWR, Najera (1994; see also Zwank et al. 1997) caught jumping mice through
356   September and until 22 October, though all were considered young of the year in these months

357   except an adult female (24.0 g) on 12 September and an adult male that weighed 32.0 g on 27
358   September and 35.0 g on 1 October, and was imminently ready for immergence (Table 3). Wright
359   (2012) did not catch any jumping mice at BANWR in September, but caught a 20.0 g young of the
360   year female on 22 and 25 October. This jumping mouse was radio-collared and its last above
361   ground movement was 26 October (Wright 2012). No jumping mice have been detected above
362   ground at BANWR between 27 October and 13 May, despite 1,740 trap-nights (1 trap-night = 1 trap
363   set for 1 night) by Najera (1994) in March, April and November and an effort of 7,540 trap-nights
364   during relatively warm spells throughout this period (Wright and Frey 2010; Wright 2012).

365   Among specimens from montane populations, only 14% were captured after August (Table
366   1). Of specimens of known age, older adults were not detected above ground after 7 September,
367   and the last recorded capture was 19 September (Figure 1). However, three specimens of unknown
368   age class were caught in October, including 4, 19, and 26 October, all from the White Mountains,
369   Arizona (Table 1). At Fenton Lake, Morrison (1987) caught 5 jumping mice in October that
370   previously had been captured with the last caught on 3 October after which trapping ended. Thus,
371   there could have been later dates of activity. Morrison (1987) thought that most adults had entered
372   hibernation by mid-September and that later occurrences were young of the year. However, in the
373   White Mountains near Greer, I caught five jumping mice on 12 September, which included four
374   young of the year weighing < 20 g, and one adult female that weighed 34 g that was imminently
375   ready for hibernation.

376   To summarize available information on immergence dates for *Z. h. luteus*, in both valley and
377   montane populations older adults disappear from the trappable population during early
378   September, while young of the year do not disappear until late October. Among adults, most above
379   ground activity during the later part of the active season appears to be females, perhaps
380   representing individuals that reproduced. Due to limitations of the available data, it is not possible
381   to determine when animals begin immergence. It is possible immergence of adults could occur as
382   early as August, as occurs in some adult *Z. h. preblei* (Meaney et al. 2003). Research on some other
383   species of mammals has shown that local climate conditions may influence whether individuals
384   hibernate or not during winter (e.g., Davis 1976, Lehmer et al 2006) and it has been speculated that
385   *Z. h. luteus* may not hibernate at BANWR given the relatively warm climate (Morrison 1988, Najera
386   1994, Najera et al. 1994). However, based on a lack of detectable above-ground activity during the
387   winter, jumping mice at BANWR probably do hibernate and the population had an active interval of
388   162 days (= ca 5.5 months) in 2010 (Wright 2012). The active interval for montane populations
389   cannot be as precisely determined, but is ca 124 – 135 days (ca 4 to 4.5 months) for Fenton Lake
390   (13 June to probably mid-October).

391   **Reproduction at BANWR**

392   The most well studied population of *Z. h. luteus* is at BANWR. At this location, most
393   pregnancies occur in late June and July. Wright (2012) caught females with corroborating evidence
394   of pregnancy on 23 June, and 20, 25, 26, and 27 July (Supplemental Table 1). For radio-collared
395   jumping mice, parturition dates probably coincided with retreat to underground burrows on 28
396   and 30 July (Supplemental Table 1). Hence, back calculated conception dates are 7 and 9 July, and
397   juveniles from those litters would be weaned and become part of the trappable population on 25

398   and 27 August, respectively. There may be some variation in these dates because some of the
399   radio-collared pregnant jumping mice had unusual and reduced activity just prior to retiring in the
400   underground burrows and it is conceivable that they gave birth outside the burrows and then
401   moved the young or conversely they retired to the burrow just prior to giving birth. Data from
402   Najera (1994) support late June through July as the primary period for pregnancy at BANWR. A
403   29.0 g female appeared pregnant on 9 July and was recaptured at least 7 days later (no date given)
404   and appeared to be no longer pregnant but lactating (Najera 1994). Females captured that were
405   evaluated as both pregnant and with large body mass (> 22 g) included two on 15 July 1991 (25.0
406   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
407   16 July 1992 (26.0 g) (Najera 1994).

408   The earliest date of pregnancy recorded at BANWR is a 21.5 g female was captured on 15
409   June 2014 that was confirmed pregnant through palpation of embryos and presence of enlarged
410   nipples (BANWR 2014). Two additional female jumping mice (23.5 g and 26.5 g) were caught on 19
411   June and confirmed pregnant by palpation of fetuses, and presence of enlarged nipples and vulva
412   (BANWR 2014). In addition, Najera (1994) caught an 8 g juvenile male (age 21- 30 days according
413   to Quimby 1951) on 31 July, that likely would have had been conceived 10 - 19 June (Najera 1994).
414   Given that there is a lag between conception and ability to detect pregnancy, pregnancies may occur
415   as early as the first week of June at BANWR.

416   Najera (1994) and Zwank et al. (1997) suspected that breeding at BANWR took place as late
417   as August because they caught young of the year animals in October. However, this estimate of
418   breeding date may be incorrect. The size range of jumping mice they caught in October was 15.0 to
419   24.5 g (mean 18.5 g). These included a 15.5 g female on the last date (22 October) jumping mice
420   were caught. According to Quimby (1951), this female was approximately 70 days old and hence it
421   had a back-calculated parturition date of 13 August and conception date of 23 July. Thus, no
422   breeding (i.e., conception) is verified after July at BANWR, though some females may not give birth
423   until early August. Similarly, at BANWR males with scrotal testes were captured most frequently in
424   June and July, with a smaller proportion in May; none were found after July (Najera 1994, Wright
425   2012).

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

433   To summarize reproductive information for BANWR, some males start to become
434   reproductively active in May, with higher proportions becoming reproductively active in June and
435   July (Figure 4). Pregnant females are known from 15 June to 27 July. Other evidence suggests
436   conception during the first and second week of June. There is no convincing evidence for
437   pregnancies in May and no reproductive activity is verified for later than 25 August (Supplemental
438   Table 1). Independent young first appear in August. However, it should be cautioned that these

439   dates are conservative given the small sample sizes. The earliest verified date of capture for a
440   young of the year is 31 July.

Reproduction in other populations

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

454   Dates for pregnancies in montane populations are generally later than in valley populations
455   (Figure 4). At Fenton Lake in the Jemez Mountains, Morrison (1987) evaluated males as scrotal
456   between 23 June and 18 July, females as pregnant between 28 July and 15 August, and females
457   having enlarged mammae between 21 July and 29 August. However, in the Jemez Mountains I
458   captured a 22 g female on 1 July that was carrying six 2 mm embryos and a 18.5 g female on 5 July
459   that was carrying six 6 mm embryos. Females specimens with embryos were captured 22 July-16
460   August (average date 27 July; N = 9) in the White Mountains and 15 July-17 August (average date
461   26 July; N = 9) in the Sacramento Mountains. Based on age class data, young of the year in montane
462   areas enter the trappable population about 17 August (Figure 1).

463   To summarize, reproductive data for populations other than BANWR are sparse and mostly
464   provide a range of dates based on confirmed or inferred reproductive status. Data are particularly
465   sparse for other valley populations, where pregnancies are inferred to have occurred as early as the
466   first week in June based on back-calculated dates. It is assumed that most pregnancies occur during
467   June and July as at BANWR. However, there is a single record of a pregnancy from as late as 19
468   August. This female was an older adult and hence this represents an exceptionally late litter. For
469   montane populations, pregnancies occur at least 2 weeks later than generally occur at BANWR,
470   with confirmed pregnancies documented from 1 July to 17 August.

Bosque del Apache summer activity hiatus

472   BANWR is the southernmost location for *Z. h. luteus* along the Rio Grande and the lowest
473   elevation location (i.e., highest temperature equivalent) where the species is currently known to
474   persist. Field studies at BANWR have revealed a sharp reduction in detectable above-ground
475   activity of jumping mice during late summer. In 1991 and 1992, Najera (1994) caught jumping
476   mice in June, July, September and October, but caught none 16 July - 10 September, which included
477   a sampling effort of 4,708 trap-nights in August (Najera 1994). In 2009 and 2010, Wright (2012)

478   captured only a juvenile male on 16 August during a 30 July - 17 August 2009 trapping period with
479   an effort of 2,910 trap-nights and a 16 g male on 28 August during a 23 August - 20 September
480   2010 trapping period with an effort of 4,320 trap-nights (Table 3).

481   **Discussion**
482   *Zapus h. luteus* exhibits geographic variation in phenology of key life history events.
483   However, not all expectations were observed and the phenology of hibernation and reproduction in
484   *Z. h. luteus* was fundamentally different compared to other subspecies of *Z. hudsonius* (Figure 4). As
485   expected, montane populations experienced later first emergence from hibernation in comparison
486   with valley populations. However, contrary to expectations, last immergence into hibernation
487   occurred at about the same time for both valley and montane populations, though immergence
488   dates were difficult to precisely define due to data limitations. Consequently, as expected, the
489   active interval was shorter for montane populations in comparison with valley populations and the
490   number of litters possible per year was reduced from conceivable two per year in valley
491   populations to only one per year in montane populations. Among populations of *Z. h. luteus*, the
492   population occurring at BANWR, which was the warmest location, had a phenology most similar to
493   other subspecies of *Z. hudsonius*. The active interval at BANWR (162 days) was the same as for *Z.*
494   *hudsonius* from central Michigan (Muchlinski 1988). However, the timing differed. Jumping mice at
495   BANWR emerged ca 4 weeks *later* than those in Michigan, which usually emerge in late April
496   (Nichols and Conley 1982, Muchlinski 1988). Rather, the timing of emergence in *Z. h. luteus* at
497   BANWR (13 May, 18 May) was similar to *Z. h. preblei* from foothills of the Rocky Mountain Front
498   Range (19 May), although *Z. h. luteus* remains active longer in the fall compared to *Z. h. preblei* (last
499   recorded above ground activities were 15 October and 26 October for *Z. h. preblei* and *Z. h. luteus*,
500   respectively) resulting in a slightly longer active interval for *Z. h. luteus* (Meaney et al. 2003). Prior
501   studies have indicated that emergence in jumping mice is cued by soil temperature (Cranford 1978,
502   Muchlinski 1988, French and Forand 2000), which is a product of the radiation regime, moisture
503   content, and snow cover of a location (Baker 1971). Although soil temperatures are not available,
504   the mean date of last spring freeze (ca 10 May; The Climate Source 2000) is similar for BANWR, the
505   Front Range, and central Michigan. Thus, the stark difference in emergence dates between
506   subspecies of *Z. hudsonius* from the Rocky Mountain region and the eastern U.S. might relate to an
507   unknown environmental variable or to adaptive evolutionary differences.

508   The greatest deviation from the typical active season pattern of *Z. hudsonius* in the eastern
509   U.S. was observed for montane populations of *Z. h. luteus* (Figure 4). Montane populations of *Z. h.*
510   *luteus* had an active interval of ca 124-135 days, which was reduced by ca 4-5.5 weeks compared
511   with eastern U.S. *Z. hudsonius* (162 days) and by ca 2-3.5 weeks compared with *Z. h. preblei* (150
512   days). Rather, the active interval was similar to populations of *Z. princeps* occurring at similar
513   elevations (2,591 m) but further north in Wyoming (124 days; Brown 1967). However, again, the
514   timing was different. In part, *Z. princeps* copes with the short summers of high elevation montane
515   sites by hibernating early, with the last individuals captured in early to mid September (earlier at
516   higher elevations). In addition, *Z. princeps* emerges from hibernation 4-8 weeks later than eastern
517   U.S. *Z. hudsonius*. At the lowest elevations (2,591) *Z. princeps* emerges from hibernation in mid May
518   (16 May), nearly identical to the population of *Z. h. luteus* at BANWR (Brown 1967). However,

519   populations of *Z. princeps* at 2,896 m emerge on 1 June, and those at 3,200 m on 13 June (Brown
520   1967). Thus, montane populations of *Z. h. luteus* emerge from hibernation as late as very high
521   elevation populations of *Z. princeps*. But, unlike the truncated activity period in fall experienced by
522   *Z. princeps*, young of the year *Z. h. luteus* from montane locations may not enter hibernation until
523   October, like *Z. h. preblei* (Meaney et al. 2003). Thus, different species and populations of jumping
524   mice adjust to short activity intervals in different ways.

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

544   The situation at BANWR is more complicated. This population of *Z. h. luteus* has an active
545   interval equivalent to eastern U.S subspecies and it is slightly longer than for *Z. h. preblei.* In
546   addition, it has a reproductive phenology similar to *Z. h. preblei* (Meaney et al. 2003). In both *Z. h.*
547   *preblei* and eastern subspecies of *Z. hudsonius* there are two peaks in reproduction (Meaney et al.
548   2003). In eastern subspecies, females can give birth to two (possibly three) litters per year (Nichols
549   and Conley 1982). Given similarity of the active season between *Z. h. preblei* and eastern U.S. *Z. h.*
550   *hudsonius*, it is commonly believed that *Z. h. preblei* also can produce two, and possible three, litters
551   per year (e.g., Armstrong et al. 2011). However, I am not aware of any published reports
552   confirming more than one litter per year in *Z. h. preblei*. Likewise, I found no evidence for more
553   than one litter per year in *Z. h. luteus*, although it seems conceivable given similarity in length of the
554   active season compared to eastern U.S. subspecies. Regardless, with two peaks in reproduction,
555   populations of *Z. hudsonius* are expected to expand following the second peak due to a pulse of
556   young of the year animals entering the population (Nichols and Conley 1982; Meaney et al. 2003).
557   However, field studies on *Z. h. luteus* conducted during the last two decades found no detectable
558   expansion of the population during summer, though there is a small pulse of presumably late litter
559   young at the end of the active season (Table 3). Though sample sizes are small, this suggests that
560   there may be little regular production of the crucial early litters at BANWR.

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

577   For the population of *Z. h. luteus* at BANWR, several factors may account for paucity of
578 detectable above ground activity during August and September. First, adult females might be in
579 nests with nursing young during August (Figure 4). However, if a large proportion of females were
580 nesting in August we would expect a pulse of young of the year in the trappable population in
581 September. That this happens is suggested by the older specimen data, but not for the more recent
582 field studies (Table 3). Data from Najera (1994) revealed that relative abundance (captures per
583 100 trap-nights) was highest in May (0.76), which tapered off in June (0.32) and July (0.24), and a
584 second minor peak in September (0.08) and October (0.33). In the study by Wright (2012) there
585 was no obvious second peak; relative abundance varied from 0.33 during 12-29 May, 0.42 during
586 11 June -8 July, 0.27 during 20 July-17 August, 0.02 during 23 August-30 September and 0.05
587 during 1-25 October. Second, as in the edible dormouse (*Glis glis*), it is possible that some females
588 die due to depletion of energy reserves during reproduction (Bieber et al. 2014). However, this
589 would not account for lack of detectability of other demographic groups. Third, as in the western
590 harvest mouse (*Reithrodontomys megalotis*), it is possible that animals change behavior during mid-
591 summer to become more scansorial within the herbaceous vegetation (i.e., "herbeal" sensu Wright
592 and Frey 2014), which might reduce capture rates in traps set on the ground (Cummins and Slade
593 2007). However, based on observations made during a radio-telemetry study, *Z. h. luteus* appeared
594 highly scansorial while foraging throughout the active season (Wright and Frey 2014). Thus, there
595 is no reason to presume capture rates would change based on a seasonal change in locomotion.

596   A fourth possible explanation for the paucity of detectable above ground activity during
597 August and September is that adult males and non-reproductive adult females might enter a
598 prolonged torpor during summer, which may or may not be confluent with winter hibernation.
599 Prolonged torpor during hot periods is called estivation, although physiologically it is similar to
600 hibernation during a cold period (Davis 1976. Geiser 2010). In some species annual hibernation
601 routinely begins as early as August within some demographic groups (e.g., Dobson et al 1992,
602 Sheriff et al 2011). In other hibernating species, a hiatus of aboveground activity or summer torpor

603   may occur as a result of drought, failure to reproduce, or failure of key food resources (Munro et al
604   2008, Bieber and Ruf 2009). Ecologically, torpor also is beneficial to hibernating small mammals
605   because it usually confers higher survival rates due to reduced predation (Bieber and Ruf 2009,
606   Turbill et al. 2011, Bieber et al. 2014). Thus, a longer growing season at BANWR that permits
607   earlier reproduction relative to other populations of *Z. h. luteus*, might allow adults the luxury to
608   enter hibernation earlier than other populations. However, there is a tradeoff between lower
609   mortality rates during hibernation and a reduced opportunity for breeding. Thus, such a strategy
610   may prove maladaptive if there is a decline in production of early litters and animals hibernate
611   early rather than produce a late litter. Given similarity of climate, it is possible that other
612   populations in the middle Rio Grande and Verde River exhibit the same pattern. Similarly, summer
613   torpor may explain why *Z. h. luteus* has become undetectable at certain locations during excessively
614   dry conditions (e.g., Frey 2013). Behavioral changes that reduce capture probabilities, such as
615   animals becoming more scansorial or estivating, can be misinterpreted as temporary emigration
616   (Cummins and Slade 2007). Thus, high rates of temporary emigration reported for *Z. h. preblei*
617   (Meaney et al. 2003) may need to be reconsidered in light of possible estivation or other behavioral
618   changes.

Management Implications

620   It is unknown to what extent the variation observed in phenology of hibernation and
621   reproduction in populations of *Z. h. luteus* is a product of selection or phenotypic plasticity.
622   Evolutionary control of hibernation is indicated by similarity of patterns in closely related species
623   (Ruf and Geiser 2014). However, studies on other species of small mammals have shown that
624   populations living in nearby but different environments are able to use phenotypic plasticity to
625   adjust phenology in largely predictable ways (e.g., Dobson et al 1992, Lehmer et al. 2006, Sheriff et
626   al. 2011). Thus, it is hoped that species can adapted to changes in environmental phenology due to
627   a changing climate through phenotypic plastic or microevolution (Boutin and Lane 2013).
628   Ultimately, resilience of *Z. h. luteus* to environmental change may be linked to how well it can adjust
629   timing and duration of life history events. However, a recent review of climate-mediated changes in
630   the phenology of mammals found limited evidence for contemporary microevolution and relatively
631   many instances of non-adaptive plastic responses (Boutin and Lane 2013). Mis-matches in the
632   phenology of an animal with its food plants or other key resources can cause non-adaptive changes
633   that can result in reduced survival and reproduction. Any such changes could pose a significant
634   threat to populations of *Z. h. luteus*, which are already small and isolated. Thus, more research is
635   needed on timing of life history events and reproduction in *Z. h. luteus* including within each sex
636   and among populations that represent a range of latitudes and elevations. Special attention should
637   be paid to linkages between the phenology of food plants with reproductive success and linkages
638   between overwinter survival and body condition with subsequent reproduction.

639   Compliance surveys, which have the objective of determining presence or absence of *Z. h.*
640   *luteus* at a project site must occur during times when animals are reliably detectable, if present. I
641   recommend that such surveys occur after all overwintering adults have emerged from hibernation,
642   which may take several weeks following first emergence. In addition, surveys conducted in late
643   summer or fall should consider that adults might enter hibernation in August and that only late

644 litter young of the year are active into fall. Thus, for most populations except in the middle Rio
645 Grande valley, I recommend that compliance surveys are best implemented in July and August. In
646 some cases it might be justifiable to survey montane locations during the last week in June or first
647 two weeks of September, but such surveys might offset lower abundances with a larger sampling
648 effort (i.e., larger number of trap-nights) over more nights. In the middle Rio Grande valley, and
649 possibly other locations with a relatively high temperature equivalent (Table 2), I recommend that
650 compliance surveys are best implemented during the last week in May through July. However,
651 during years when winter weather occurs later than usual in the spring which may result in delayed
652 emergence of *Z. h. luteus*, the start date for surveys also should be delayed.

Acknowledgments

654   I am grateful to Greg Wright for his assistance and the many insightful discussions we have
655 had about jumping mice. I thank Scott Wait of Colorado Parks and Wildlife and Jennifer L. Zahratka
656 for providing information about jumping mice at Sambrito Creek. I thank Christina Kenny for
657 assistance creating the histograms. I thank F.S. Dobson, an anonymous reviewer, and the academic
658 editor, D. Kramer, for constructive suggestions that improved the paper.

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Table of records of jumping mouse specimens by month

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 of predicted dates of first emergence

Latitude, longitude, elevation, temperature equivalent, and predicted date of first emergence of the 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	North latitude (degrees)	West longitude (degrees)	Elevation (m)	Temperature Equivalent (C°)	Predicted date of first emergence	Earliest known dates
Verde River, Camp Verde[a]	34.6	111.8	950	19.4	6 May	
Rio Grande, Bosque del Apache	33.8	106.9	1,370	16.8	14 May	13 May, 18 May
Rio Grande, Isleta	34.9	106.7	1,495	15.2	18 May	24 May
Rio Grande, Espanola	36.0	106.1	1,700	13.1	25 May	24 Jun
White Mountains, Campbell Blue Creek	33.7	109.1	2,000	12.2	28 May	
Sacramento Mountains, Tularosa Creek	33.1	105.7	2,050	12.2	28 May	18 June
Sacramento Mountains, Rio Penasco	32.8	105.6	2,170	11.5	30 May	
Piedra River, Sambrito Creek	37.0	107.5	1,860	11.5	30 May	21 May[b]
Florida River, Florida	37.2	107.7	2,050	9.9	4 June	
White Mountains, West Fork Black River	33.8	109.4	2,330	9.8	5 June	20 June
Mora River, Mora	36.0	105.3	2,185	9.6	5 June	
White Mountains, Nutrioso Creek	33.9	109.2	2,450	8.8	7 June	
Sangre de Cristo Mountains, Fort Burgwin	36.3	105.6	2,250	9.0	7 June	
Jemez Mountains, Fenton Lake	35.9	106.7	2,350	8.5	9 June	13 June
White Mountains, North Fork White River	34.0	109.7	2,500	8.4	9 June	24 June
Jemez Mountains, San Antonio Creek	35.9	106.6	2,355	8.4	9 June	28 June
Sacramento Mountains, Aqua Chiquita Creek	32.7	105.7	2,600	8.4	9 June	
Sangre de Cristo Mountains, Sugarite Canyon	37.0	104.4	2,300	8.2	9 June	11 June
Sangre de Cristo Mountains, Coyote Creek	36.2	105.2	2,365	8.2	10 June	
Sacramento Mountains, Wills Canyon	36.8	105.7	2,680	7.8	11 June	
Sangre de Cristo Mountains, Rito la Presa[c]	36.1	105.5	2,670	6.0	16 June	
White Mountains, Lee Valley Creek	33.9	109.5	2,880	5.7	17 June	
Sangre de Cristo Mountains, Rio Hondo[c,d]	36.6	105.4	2,870	4.3	22 June	

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

[b]Trapping started 20 May; 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 of age of jumping mice by month at BANWR

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.

Month	Museum specimens[a]			Najera (1994); Najera et al. (1994)[b,d]		Wright (2012); Frey and Wright (2012)[c,d]	
	Age class < 0.35	Age class = 0.35	Age class > 0.35	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	9	1	0	0	2	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. Age class < 0.35 were considered young of the year; age class 0.35 were considered older young of the year immerging into hibernation and emerging from hibernation during their second active season; age class > 0.35 were older adults.

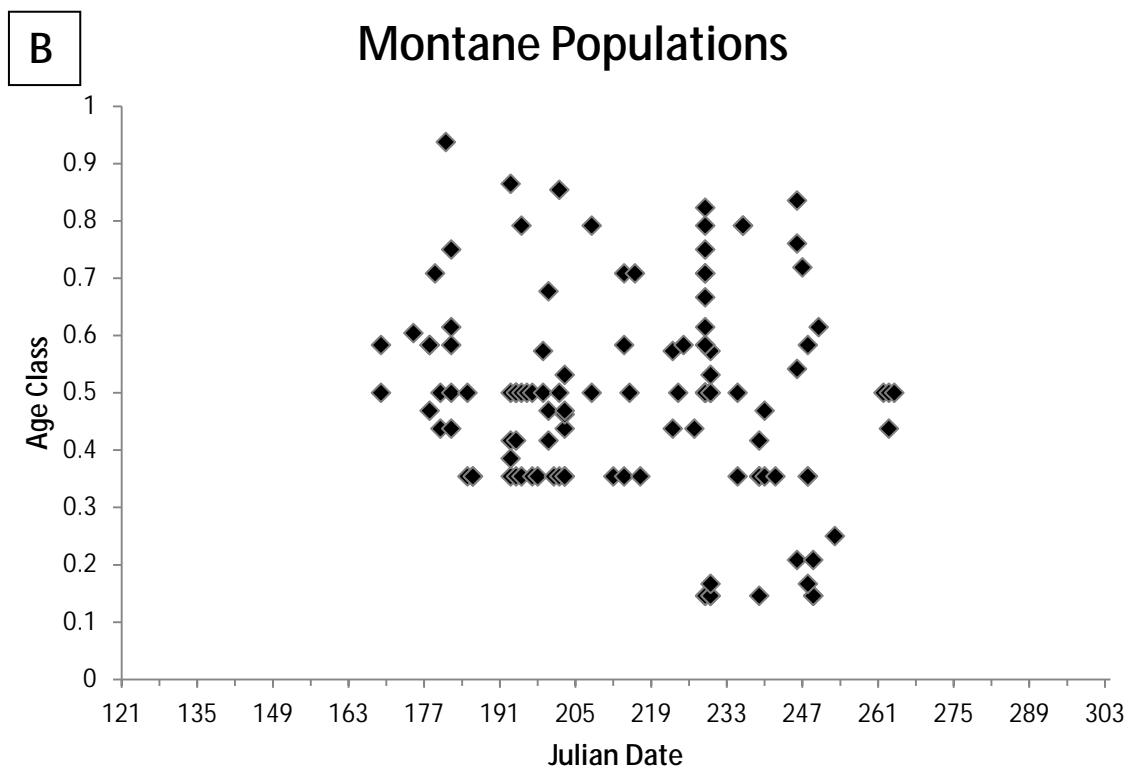
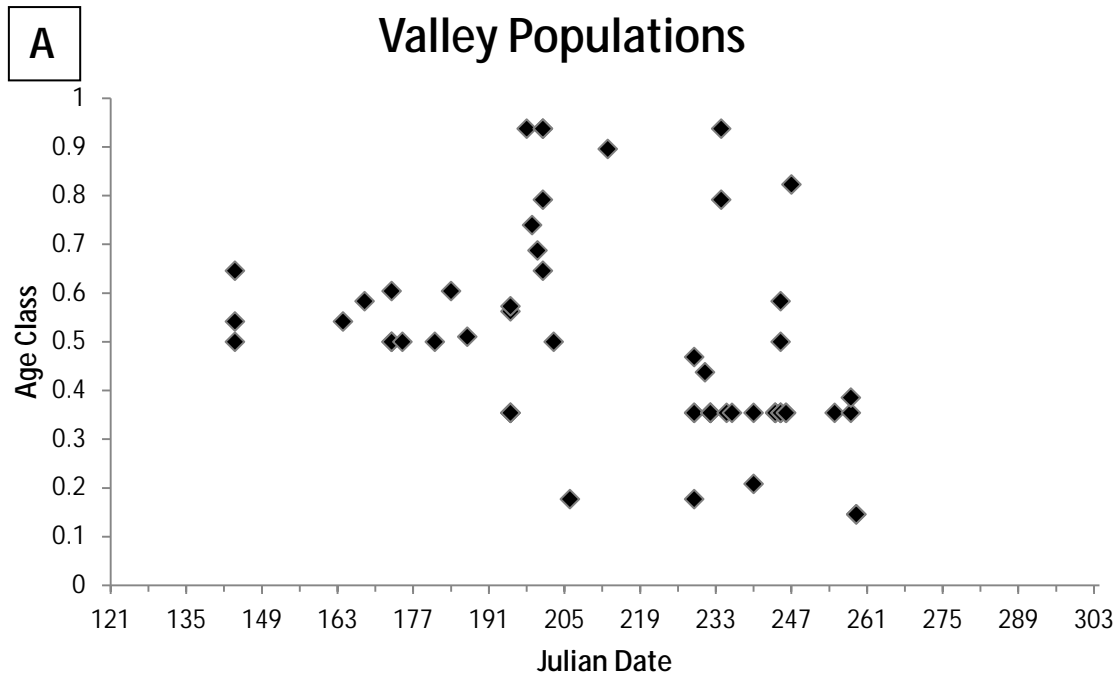
[b]Results are combined for data collected June-October 1991 and May-July 1992.

[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.

Figure of age class of jumping mouse specimens by date of capture

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

Histogram of male and female jumping mouse capture dates by week

Activity season of male (black bars) and female (white bars) New Mexico meadow jumping mice (*Zapus hudsonius luteus*) from A) valley populations and B) montane 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.

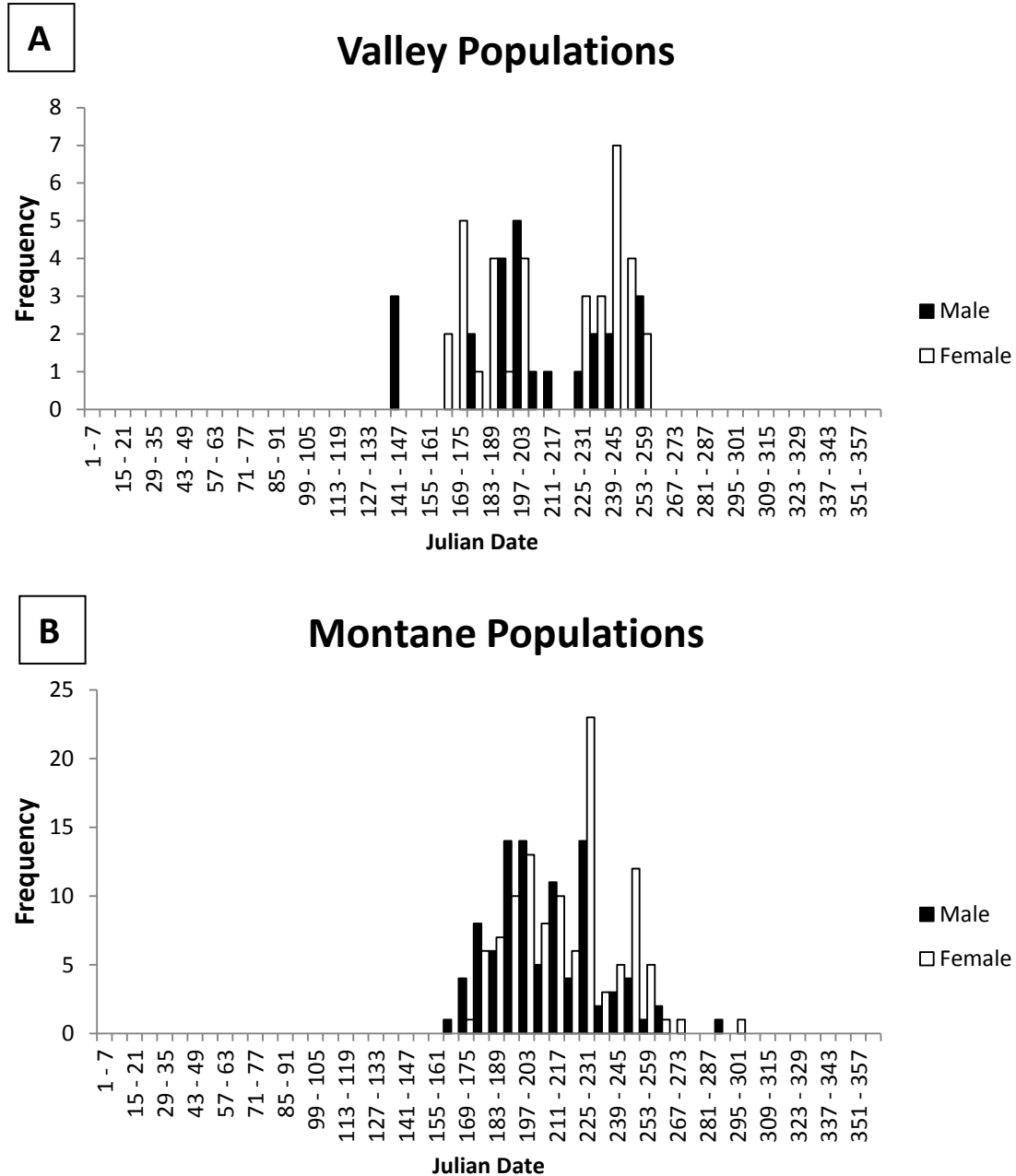
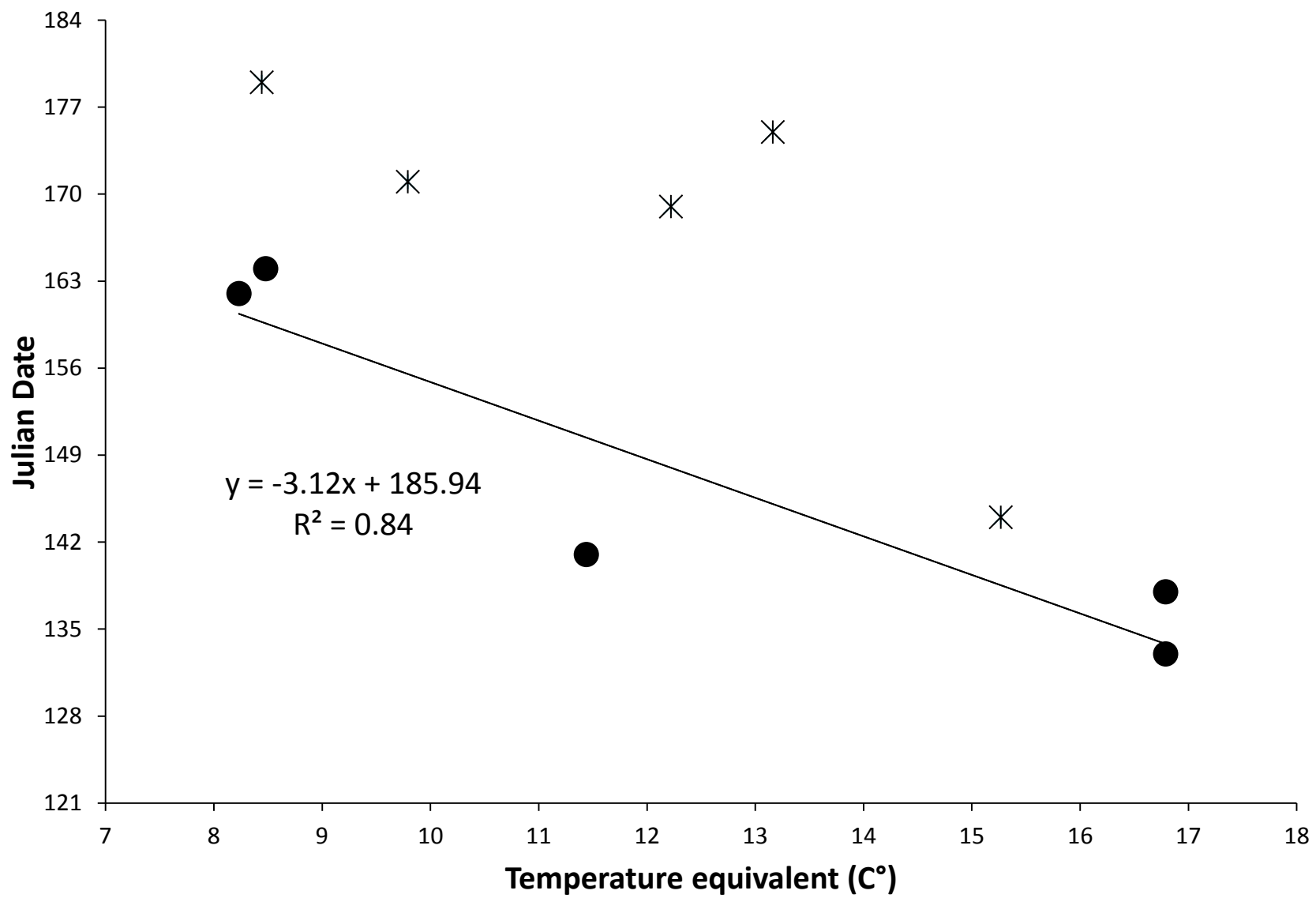



Figure of relationship between temperature equivalents and date of first emergence

Relationship between the temperature equivalent (C°) of a location and the earliest known date for emergence of the New Mexico meadow jumping mouse (*Zapus hudsonius luteus*) from hibernation. Temperature equivalents are relative to a hypothetical location with approximate average conditions for New Mexico: 34°N latitude, 1,981 m elevation, and mean annual temperature of 12.2°C. Solid dots and regression line are based on dates of earliest capture during field studies; stars are earliest dates of representative museum specimens. Julian dates range from 1 May (121) to 3 July (184).

Schematic of timing of hibernation and reproduction

Generalized schematic of the timing of key life history events for the New Mexico meadow jumping mice (*Zapus hudsonius luteus*) at A) Bosque del Apache National Wildlife Refuge (BANWR), and B) in montane populations. Solid lines represent time frames documented by observation; dashed lines represent time frames that are inferred based on timing of other observed events. Asterisks indicate pregnant females captured at other valley locations (Sambrito Creek and Isleta) that suggest a wider possible time frame for pregnancies at BANWR.

A) BANWR

1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
May				June				July				August				September				October			

B) Montane

1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
May				June				July				August				September				October			