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Evolution of litter size in North America's most common small mammal: an informatics-based approach

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Determining the environmental and ecological drivers of variation in mammalian life histories is essential for effectively monitoring responses of these taxa to global change. We investigated relationships between climate and an integral life history trait (litter size) in the geographically widespread North American deer mouse (*Peromyscus maniculatus*). Using a spatiotemporally comprehensive data set of *P. maniculatus* embryo counts assembled from digitized museum specimens and small mammal census records (> 2,000 observations spanning more than a century), we modeled the associations of litter size with short- and long-term climate variables, and tested for shifts in litter size in response to recent climate change. Litter size in *P. maniculatus* was correlated with length of the frost-free period, suggesting the former trait may have evolved partly as a response to abiotic or resource-driven constraints on the number of annual breeding opportunities. Short-term climate variables (temperature and precipitation during breeding) were significant predictors of litter size in some models; however, all short- and long-term climate variables other than number of frost-free days added marginal predictive power. Further analyses confirmed age-structured breeding in the most seasonal regions, where maternal body sizes and litter sizes both decrease within a year, although maternal body size itself was poorly predictive of litter size in these populations. We also found a statistically significant decrease in *P. maniculatus* litter size through time and across known frost-free period regimes (pre- and post-1980), as predicted if longer frost-free periods are increasing lifetime breeding opportunities in this species, although more work is required to confirm this trend and identify underlying mechanisms. Our study refines understanding of climate impacts on *P. maniculatus* life history and reiterates the great potential of digitized specimen data to help address outstanding questions in mammalian life history and climate change response.

Key words: climate change, collections digitization, embryo, frost-free period, life history, *Peromyscus*, phenology, small mammal

Mammals show enormous variation in life history, including short-lived, iteroparous species such as shrews and many small rodents (Fleming 1979; Stearns 1983); long-lived but irregularly reproducing species such as ursids, probiscideans, and many cetaceans (McCullough 1999; Bowyer and Kie 2006); and even semelparous mammals like marsupial mice (Dasyuridae), in which males undergo just a single lifetime reproductive event (Wood 1970; Braithwaite and Lee 1979). Significant progress has been made categorizing and comparing patterns of life history variation across Mammalia (Millar 1977, 1981; Millar and Zammuto 1983; Stearns 1983; Read and Harvey 1989; Hayssen et al. 1993; Sibly and Brown 2007). However, identifying the processes responsible for evolution of key life history traits often is challenging (Millar 1977; Promislow and Harvey 1990; Innes and Millar 1994). This is especially true at shallow phylogenetic levels, where a diversity of environmental or ecological factors (e.g., climate, seasonality, resource availability, interspecific interactions) can interact to shape variation in life history traits across space and time. Establishing more robust links between these traits and the factors shaping them within and across populations is critical for effectively monitoring mammalian physiological and life history responses to global change.

One key life history trait, litter size, varies notably across extant Mammalia and is an integral parameter contributing to individual fitness as well as long-term persistence of species (Millar 1977, 1981; Hayssen et al. 1993). Optimal litter size is defined as the number of offspring that maximizes lifetime reproductive success of females (Lack 1947; Cody 1966; Sikes 1998), and is shaped by factors that modulate the number of successful lifetime reproductive efforts, such as environmental (= abiotic) variables, resource availability, the intensity of inter- and intraspecific competition for those resources, predation pressures on both adults and juveniles, and intrinsic phenotypic and genotypic traits of breeding females. In this paper, we focused specifically on that component of variation in litter size that is influenced by the abiotic environment, and which also is susceptible to altered selection pressures due to global climate and environmental change.

Lord (1960) was among the first to broadly test a litter size–environment association in mammals; he demonstrated positive correlations between embryo counts and latitude across a range of temperate North American small mammals, suggesting that litter sizes in phylogenetically disparate clades are shaped by similar abiotic factors that vary along broad spatial gradients. Although not corrected for potential biases such as phylogenetic covariance, Lord's (1960) work provided context for more detailed studies of geographic variation in litter size (based on both embryo counts and observed litter sizes) within North American small mammals. For example, Barkalow (1962) documented a positive relationship between litter size and latitude in eastern cottontails (*Sylvilagus floridanus*), and Keith et al. (1966) demonstrated a positive association of litter size and latitude in snowshoe hares (*Lepus americanus*). Millar (1989) recovered significant positive correlations between litter size and latitude in the North American deer mouse (*Peromyscus maniculatus*) and the white-footed mouse (*P. leucopus*). Likewise, Blus (1966) documented a positive relationship between litter size and latitude in the golden mouse (*Ochrotomys nuttalli*). In the southern red-backed vole (*Myodes gapperi*), Innes (1978) demonstrated positive relationships between litter size and latitude as well as elevation.

Lord's (1960) basic findings have been supported in many small mammal species, but it is noteworthy that studies of additional temperate taxa have failed to recover litter size–latitude relationships (*Sigmodon hispidus*—Bowdre 1971; *Ochotona princeps*—Millar 1973; *Microtus californicus*, *M. montanus*, *M. ochrogaster*, *M. pennsylvanicus*—Innes 1978). These results suggest that the mechanisms behind the evolution of litter size likely differ among mammal clades (as originally discussed by Lord 1960). Unfortunately, our understanding of the mechanisms underlying the evolution of litter size in many mammals remains hindered by a lack of studies considering more proximate environmental factors. Tökölyi et al. (2014) conducted a comparative analysis of mammalian life history traits in relation to climate; across much of Rodentia, they found negative correlations between litter size and both mean temperature and precipitation, but positive correlations between litter size and temperature variation and seasonality. Unfortunately, few comparably detailed attempts have been made at the intraspecific level in rodents, and fewer have focused on how recent changes in environmental factors might be impacting variation in litter size.

Peromyscus maniculatus (Cricetidae: Neotominae) is a small-bodied rodent distributed across much of North America, from central Mexico to near tree line in the Canadian high arctic (Osgood 1909; Baker 1968; Hall 1981; Carleton 1989). *Peromyscus maniculatus* likely is the most common small mammal in North America; it is geographically widespread and has been documented as the most abundant element of mammal communities in many parts of its range (Osgood 1909; Calhoun and Arata 1957a; Baker 1968; Hall 1981). A substantial literature exists describing life history variation among *P. maniculatus* and its congeners (e.g., Terman 1966; Layne 1968; Modi 1984; Glazier 1985; Bronson and Perrigo 1987; Millar 1989). Several studies have examined patterns of variation in litter size specifically, and some have recovered positive associations with latitude (McLaren and Kirkland 1979; Millar 1989), elevation (Dunmire 1960; Spencer and Steinhoff 1968), or both (Smith and McGinnis 1968). Millar (1989) analyzed the most spatially comprehensive litter-size data set to date and demonstrated positive associations between litter size and both latitude and longitude in *P. maniculatus*. However, each of these studies employed indirect proxies (e.g., latitude) of the actual environmental variables likely to be shaping litter size in *P. maniculatus*. As Millar (1989:193) noted: "It should be remembered that organisms do not respond to latitude, longitude, or elevation per se. Comparisons should involve meaningful measures of the environment."

Herein, we evaluated the ability of such measures to explain variation in litter size in *P. maniculatus*. We assembled and curated new data sets describing variation in litter size (specifically, embryo counts) across the range of this species from digitized natural history specimen records and published historic small mammal censuses. Natural history specimens in particular are a promising and typically precise source of mammalian life history trait data; however, digitization and mobilization of these data are ongoing, which has limited their utility for testing ecological and evolutionary hypotheses. We paired this litter-size data set with historic temperature and precipitation variables inferred at the time and place of capture, resulting in the most spatiotemporally resolved database ever leveraged to investigate patterns of litter-size variation in *P. maniculatus*. Using regressions, we tested the association of litter size with multiple biologically relevant climate variables and body size, and evaluated support for competing models in a model-selection framework. We also investigated how maternal body size and age-structured breeding regimes themselves vary within different climate zones, and potential impacts of these factors on litter size. Finally, we used our data set to test a hypothesis of recent shifts in litter size in *P. maniculatus* in response to recent increases in length of the frost-free period in North America.

MATERIALS AND METHODS

Data sources.—We used embryo count data from individual *P. maniculatus* as a proxy for litter size. Embryo count is a common reproductive parameter recorded during traditional sampling and preservation of wild mammals, and is simply the total number of developing embryos observed in the female uterus upon autopsy. Most metrics of uterine condition (including embryo count, placental scarring, or embryo size, typically expressed as a single measurement: crown-rump length) can be easily and accurately collected macroscopically, but in some cases microscopic examination may also be used.

Embryo counts are not an exact measure of the number of successfully birthed young, despite their wide use in comparative studies of litter-size variation in mammals. Embryo counts are known to be slightly greater on average than the number of birthed young due to embryo loss or resorption (Svihla 1932; Beer et al. 1957). Embryo counts from late-term pregnancies may also be inflated relative to early-term pregnancies (Beer et al. 1957; Loeb and Schwab 1987) due to more frequent termination of late-term fetuses. In either case, the average maximum error in embryo counts within populations of *Peromyscus* (across gestation stage or parturitions) has typically been found to be one or less (Coventry 1937; Beer et al. 1957; Dunmire 1960; Loeb and Schwab 1987).

The difference between litter size and embryo count in *Peromyscus* species may relate to effects of individual age, body size, and time of year (Svihla 1932; Beer et al. 1957; Myers and Master 1983; Loeb and Schwab 1987; Havelka and Millar 2004), but there is no single correction that has been developed in order for embryo count data to better reflect actual birthed litter sizes. We therefore use "embryo count" and "litter size" interchangeably in this paper, but acknowledge embryo counts to be a consistently (but slightly) inflated proxy for female reproductive output in some populations. We note that use of embryo counts allows our results to be placed within a wide range of previous life history studies in *Peromyscus* (e.g., Dunmire 1960; Lord 1960; Smith and McGinnis 1968; McLaren and Kirkland 1979), while also providing increased rigor relative to studies that have combined data from litter sizes, embryo counts, or placental scars, as well as data from wild and laboratory colonies.

Embryo counts for *P. maniculatus* were obtained from two primary sources. First, we used digitized natural history specimen records aggregated in VertNet (vertnet.org—Guralnick and Constable 2010; accessed November 2017). We performed a general taxonomic search ("*Peromyscus maniculatus*") in VertNet and downloaded all resulting records. To identify records of females containing relevant reproductive information, we used base regular expression matching functions in R (R Core Team 2017), specifically searching across five Darwin Core (DwC—Wieczorek et al. 2012) fields ("dynamic properties," "reproductivecondition," "occurrenceremarks," "highergeography," "scientificname") for matches to 14 expressions commonly employed to encode female reproductive state in mammals (e.g., Kunz et al. 1996; Taber 1969; "litter," "scar," "plsc," "plac," "emb," "fetus," "fetal," "preg," "CR=," "partu," "parous," "parity," "corpor," "lutea"). The five DwC fields we queried were identified in preliminary data scans as those most likely to contain reproductive information for this species.

We extracted specimen records with positive matches to at least one reproductive search term into a reduced data set. We then cleaned this reduced data set of records known or likely to represent captive individuals; specifically, we omitted any record explicitly encoded as a captive in DwC terminology (i.e., DwC field "wascaptive" = 1). However, because digitization norms are heterogeneous across institutions and all captive individuals may not be encoded in this way, we also scanned DwC fields of the remaining records for matches to at least one of eight regular expressions used to describe such individuals ("captive," "colony," "stock," "lab stock," "laboratory stock," "strain," "reared," "raised"). Expression matches were vetted manually, and all positive matches were omitted from the data set. We then manually extracted standard embryo counts from all remaining records. In addition, we extracted body size information from these records in the form of total lengths and tail lengths, which we used to derive head-body lengths. For several hundred records in the embryo count data set without body length data, we requested this information from collection managers at respective museums.

The second source of embryo count data we used was the North American Census of Small Mammals (NACSM—Calhoun 1948, 1949, 1950, 1951, 1956; Calhoun and Arata 1957a, 1957b, 1957c, 1957d). NACSM was a program of the Rodent Ecology Project at Johns Hopkins University; the aim of the NACSM was to coordinate small mammal trapping efforts at sites across North America in order to understand local- and continental-scale fluctuations in small mammal populations (Calhoun 1948). We consulted annual NACSM reports and manually digitized all records of pregnant *P. maniculatus*. In addition to embryo counts, we digitized verbatim locality, elevation, trap date, and external body measurements (if available) for pregnant females.

Next, we obtained geocoordinates for all embryo count records in the combined VertNet + NACSM data set. For VertNet records that contained associated geospatial data, we used those geocoordinates verbatim after screening for spatial outliers lying significantly beyond the known geographic range of *P. maniculatus*. We manually georeferenced all other embryo count records. Georeferencing protocols followed Chapman and Wieczorek (2006) and employed a combination of tools including Google Maps (https://www.google.com/maps), the MaNIS georeferencing calculator (Wieczorek et al. 2001; http://manisnet.org/gci2.html), and occasionally the USGS Geographic Names Information System (for historic place names only; https://geonames.usgs.gov/domestic/).

We obtained paired historical climate data for all georeferenced embryo counts using ClimateNA v5.60 (Wang et al. 2016). ClimateNA is a reference tool consisting of past and present climate grids for mainland North America interpolated from long-term weather stations using the method of Mitchell and Jones (2005). ClimateNA expands upon the PRISM data set available for the United States (http://www.prism.oregonstate.edu/) and aggregates derived historical climate data at 4-km resolution. We used specimen geocoordinates as input into ClimateNA and augmented these with verbatim elevation values for records when available; the latter values are used by the software for spatial refinement of climate estimates within grid cells. Default settings were used for all ClimateNA extractions, and all available climate variables were extracted for each embryo count record and later parsed for statistical analysis.

Model variables.—We curated a suite of biologically relevant climatic predictor variables from the raw ClimateNA extractions (Table 1). These variables included metrics of temperature, precipitation, and seasonality known to influence large-scale biological processes (Hijmans et al. 2005; Wang et al. 2016) and likely to constrain resource availability for, and survival and reproductive biology of, small mammals (Gashwiler 1979; Bronson 1985; Millar 1989; Ostfeld et al. 1996; Luis et al. 2010; Tökölyi et al. 2014). Variables ranged in temporal scope from long-term (multiannual averages at the site of collection) to more instantaneous (annual and monthly scale, representing conditions at the time and site of capture). Finally, we incorporated an individual-based phenotypic metric (head-body length) that is positively correlated with litter size in some *P. maniculatus* populations (Rolan and Gier 1967; Smith and McGinnis 1968; Myers and Master 1983; Millar 1985).

Long-term climate variables captured broad, continental-scale climate variabilities likely to be important for mammal life history (Tökölyi et al. 2014), which also may impact the number and timing of annual breeding opportunities in *P. maniculatus*. These included temperature seasonality (TS), precipitation seasonality (PS), and the number of frost-free days per year (NFFD). For each of those variables, we calculated average values for the year of collection and the preceding 9 years (resulting in a decadal average). A small number of historic records ($n = 5$) were collected prior to 1910; for each of those records we calculated decadal averages for the period 1901–1910. Because each of the long-term climate variables has a temporal grain significantly greater than the life span and gestational length of *P. maniculatus* (the latter roughly 22–30 days—Svihla 1932; Millar 1982; Modi 1984), correlations with litter size would be consistent with a genetically based mechanism of litter-size variation (adaptation) or, possibly, multigenerational responses to environmental cues (e.g., maternal effects or temporal lags in population density). In addition to capturing long-term climate variation, decadal averaging reduced potential negative impacts of short-term (e.g., annual) climate anomalies. None of our long-term variables are metrics of winter climates, even though such parameters can directly influence *P. maniculatus* life history through effects on survival and population demography. However, many winter metrics (e.g., extreme minimum temperatures, number of freezing degree days) are correlated with NFFD; thus, we view the NFFD variable as an integrative metric that captures multiple aspects of annual climate.

We employed five instantaneous climate variables that were complimentary to long-term variables in their focus, but different in temporal scope; specifically, these variables captured conditions during the copulatory and gestational periods that were experienced by individual breeding females. The first two instantaneous variables were mean temperature at breeding (TB) and total precipitation at breeding (PB). Both variables were calculated using data from the month of collection and preceding month (Table 1), which was appropriate because body condition of females and resource availability are likely a function of climates in the weeks preceding pregnancy, but also because some observations were from early in the month of collection (Supplementary Data SD2).

The third and fourth instantaneous variables were metrics of climate anomalies for the year or month of collection, respectively. The first (NFFD_anomaly) represented the deviation in number of frost-free days for the year of collection relative to the 10-year average (i.e., NFFD as calculated above). NFFD_anomaly was calculated as the difference between these two values scaled by NFFD, and the metric captured short-term deviation in growing season length that could impact the number of possible breeding attempts in the year of collection. The second variable (FDD_anomaly) represented the annual deviation in freezing degree days (FDD) in all winter months preceding the month of collection, relative to the 10-year average FDD. We used the FDD_anomaly metric to quantify the severity of winter months preceding each observed pregnancy, and followed the standard delineation of winter months in ClimateNA (only December, January, and February). For individuals collected during or after February, FDD_anomaly was calculated as the difference between total winter freezing degree days and the long-term FDD for these months, scaled by FDD. For individuals collected prior to February, we calculated freezing degree days (and FDD_anomaly) exactly as above but

Table 1.—Predictor variables used in regressions of range-wide litter-size variation in *Peromyscus maniculatus*. NACSM = North American Census of Small Mammals.

Variable acronym	Variable	Description	Classification	Source
TS	Temperature seasonality	10-year *SD* of monthly temperature (°C)	Long-term	ClimateNA
PS	Precipitation seasonality	10-year *SD* of monthly precipitation (mm)	Long-term	ClimateNA
NFFD	Number of frost-free days	10-year average of annual number of frost-free days	Long-term	ClimateNA
TB	Mean breeding temperature	Average temperature during breeding month and previous month (°C)	Instantaneous	ClimateNA
PB	Total breeding precipitation	Total precipitation during breeding month and previous month (mm)	Instantaneous	ClimateNA
NFFD_anomaly	Number of frost-free days anomaly	Annual deviation from decadal mean number of frost-free days	Instantaneous	Climate NA
FDD_anomaly	Freezing degree days anomaly	Annual deviation from decadal mean number of freezing degree days	Instantaneous	ClimateNA
DFFP	Day during frost-free period	Days elapsed after beginning of frost-free period	Instantaneous	ClimateNA
HB	Head-body length	Total length – tail length (mm)	Individual-based	VertNet, NACSM

using only the relevant months (either December, or December + January).

Finally, we developed a fifth instantaneous variable (day during frost-free period; DFFP) that quantified the date of individual capture with reference to the first day of the frost-free period for each collection year (e.g., an individual captured on the first frost-free day of the year would be assigned a DFFP value of 0). The DFFP metric served as a general proxy for changes in climate conditions and resource availability that occur across the frost-free period in most regions. However, because many temperate populations of *P. maniculatus* experience seasonal shifts in breeding age structure (early season breeding dominated by older overwintered females, late season breeding comprised of a mix of older and young-of-year females), the DFFP metric also served as a proxy for possible changes in body condition and average parity (the latter is positively correlated with age in multiple *Peromyscus* species; e.g., Millar 1982; Myers and Master 1983; Havelka and Millar 2004) that might occur in these populations across the breeding season.

The single individual-based predictor we used in this study was a phenotypic trait (head-body length; HB) describing maternal body size, which is positively correlated with maternal age and litter size in some *P. maniculatus* populations (Rolan and Gier 1967; Layne 1968; Myers and Master 1983; Millar 1985; but see Earle and Lavigne 1990). Head-body length was preferable to body mass as a size metric because our data set consists only of pregnant females, and body mass would be autocorrelated with litter size (the response variable). HB was calculated by subtracting tail length from total length for all individuals. To avoid bias in this variable from digitization or transcription errors, we screened both of the two original measurements (total, tail length), as well as the derived metric (head-body length), for measurements greater or less than three times the interquartile range, and removed as these as outliers.

Testing climatic contributions to litter size.—All climate variables were mean-centered and scaled to unit length under the two-norm prior to analysis, placing parameter estimates on the same scale and enabling direct comparisons of effect sizes within each model. We used general Poisson regressions (suitable for count data such as numbers of embryos) implemented in the glm function in R to test the association of litter size with different combinations of climate variables and HB. As a test for overdispersion of embryo count data, we inspected the ratio of residual deviance to residual degrees of freedom in each model. We also tested a null hypothesis of equidispersion from model outputs using the dispersiontest function in the R package AER v1.2-6 (Kleiber and Zeileis 2018).

We performed model selection on results from a global model and a series of submodels that allowed us to compare impacts of long-term versus short-term climate variables on litter size. For each fitted model, we calculated summary statistics (pseudo-R^2, P-value), as well as Akaike information criterion (AIC) scores as our model selection metric. We assessed model specification visually by examining scatterplots of standardized residuals versus the model fitted values as well as Q–Q plots of standardized residuals. To check for potentially harmful collinearity problems, we used the scaled condition indices of each model's design matrix and the variance decomposition proportions of each model's parameter estimates, following methods outlined in Belsley (1991). We considered model condition numbers > 30 to be evidence of harmful collinearity. Significance of all variables and the overall models themselves was assessed at the alpha = 0.05 level.

The global model contained all eight climate variables plus our single phenotypic metric (HB). Next, we ran two submodels that included 1) only long-term climate variables and HB, and 2) only short-term climate variables and HB. Due to evidence of excessive collinearity, we ran these same three models (global, long-term variables only, short-term variables only) without the HB term. Finally, to account for possible changes in demography across the breeding season that may not be captured by HB, we ran both the long-term and short-term models including the DFFP term (which may capture changes in individual-based traits such as age or parity).

Because environmental factors (e.g., soil type, land-use category, elevation) other than the climate variables we employ here could potentially impact litter sizes, we ran general linear mixed models identical to those above, but incorporating random effects designed to capture the spatial and temporal structure inherent in our sampling. We used sampling "bouts" as random effects, which we defined as unique combinations of location (0.1 latitudinal and longitudinal grid cells) and year of collection (thus, effectively a site × year effect). All observations were classified by sampling bout and mixed Poisson models were implemented using the lme4 package v1.1-19 (Bates et al. 2018) in R.

Testing demographic contributions to litter size.—In addition to tests of climate–litter size relationships, we directly tested for variation in population demographic parameters that might impact litter size. Based on previous work in highly seasonal areas (e.g., Millar et al. 1979; Havelka and Millar 2004), we expected that breeding age structure in seasonal areas would display greater intra-annual changes than in aseasonal areas. Specifically, we hypothesized that larger-bodied, overwintered females would contribute more litters early in the year and younger and smaller-bodied age cohorts would contribute more litters later in the year. We tested this hypothesis using two sequential analyses. First, we performed linear regressions of head-body length (HB) on day during frost-free period (DFFP) and number of frost-free days (NFFD), as well as their interaction term; this was a test of whether maternal body size varied with number of days during the frost-free period, and whether the magnitude of that change is related to total length of the frost-free period (and thus seasonality). To better visualize the results of these regressions, we binned records of litter size into NFFD quartiles and ran regressions of litter size on DFFP within each quartile, and also constructed boxplots of HB within the most extreme NFFD bins. Second, we performed Poisson regressions of litter size on HB and DFFP; this provided a test of whether maternal body size or some alternative DFFP-associated trait (e.g., maternal age or parity) contributed to the within-year variation in litter size that we found. Significance for all regressions was assessed at the alpha = 0.05 level.

Testing for changes in litter size through time.—Finally, we tested a hypothesis of litter-size change across the temporal span of our data. Based on the emergence of NFFD as a strong predictor in our models, we specifically hypothesized that there could be a recent decrease in litter size, as might occur if females have capitalized on longer frost-free periods (e.g., Kunkel et al. 2004) by increasing their number of annual breeding opportunities. To test for temporal change in litter size, we first split our data set into 20-year time bins (1900–1920, 1921–1940, 1941–1960, 1961–1980, 1981–2000, 2001–2020); we binned the data instead of allowing NFFD to vary continuously (e.g., by year) because the increase in frost-free days in North America over the past century has not been monotonic, thus reducing suitability of a linear model for such data. Following from the predictive power of NFFD (see "Results"), we performed a Poisson regression of litter size on NFFD and time bin (the latter as a categorical variable) as well as their interaction term (to capture the known change in frost-free period over the past century).

Due to the spatial heterogeneity in our data set through time (Supplementary Data SD4), it is possible that binning observations by 20-year intervals could introduce sampling error. Therefore, as a further test of litter-size changes through time, we re-ran identical Poisson models with observations of litter size binned into two larger time bins that correspond to distinct frost-free period regimes in North America (pre-1980, post-1980). These temporal regimes in NFFD have been identified in a series of previous studies (Kunkel et al. 2004; Barichivich et al. 2012; McCabe et al. 2015; Reid et al. 2016). Finally, to better visualize contributions of different *P. maniculatus* populations to potential temporal changes in litter size, we performed individual regressions of litter size on NFFD regime (pre-1980, post-1980) within discrete NFFD quartiles. Significance for all models was assessed at the alpha = 0.05 level.

RESULTS

Our VertNet query returned 211,688 records of *P. maniculatus*, 82,972 (39%) of which were unambiguously coded as female. Records of 6,601 females had matches to our broad reproductive terms, and 1,671 records contained unambiguous embryo counts. We manually georeferenced approximately one-quarter of these VertNet records (n = 437). In addition, 325 records of litter size were obtained from the NACSM; this represents the total number of records of *P. maniculatus* embryo counts contained in that source with sufficiently detailed locality descriptions for georeferencing. Our full data set contained spatially resolved embryo counts from 2,036 unique individuals (Supplementary Data SD1).

The geographic availability of records in our data set was variable, with particularly dense sampling in some western U.S. states including Colorado, New Mexico, and California (Fig. 1). Sampling was sparser in parts of central and southern Canada, the midwestern United States, and Mexico. Because the majority of data was from the United States (and, to a lesser extent, Canada), the latitudinal distribution

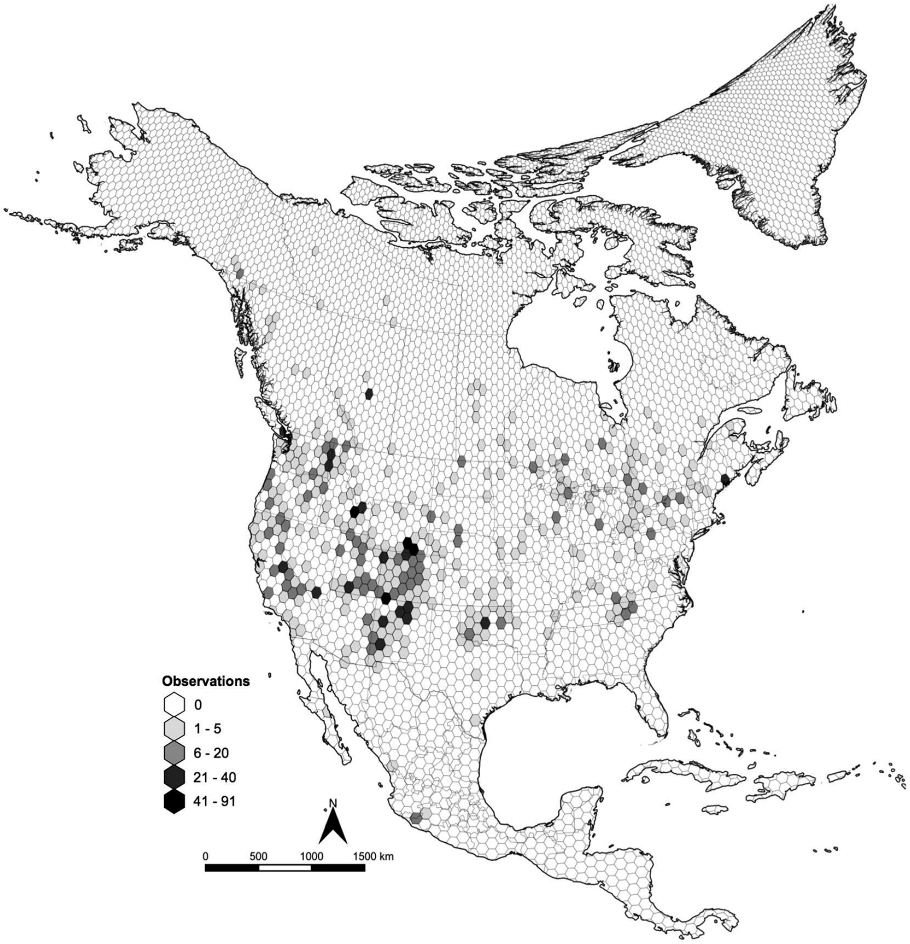

Fig. 1.—Geographic distribution of museum specimens of *Peromyscus maniculatus* used in this study. Darker colors indicate higher sampling intensity and correspond to number of observations in the legend. The map is a United States Albers Equal Area Conic projection.

of litter-size observations was peaked and slightly skewed toward higher latitudes (kurtosis = 4.35, skewness = 0.41; Supplementary Data SD3). The temporal range of records was more than a century, from 1904 to 2017, and included records from all but eight of the intervening years. The average number of records available per year was 19.39, ranging from 1 to 112 across years and increasing significantly through time ($R^2 = 0.17$, $t = 4.77$, $P << 0.01$ for all data; linear regression). There were small, but statistically significant, differences through time in the latitudinal and longitudinal scope of our data set (in both the means and variances of these values; Supplementary Data SD4).

Litter size had a significant positive correlation with latitude ($Z = 5.40$, pseudo-$R^2 = 0.04$, $P << 0.01$), but not longitude ($Z = 0.81$, pseudo-$R^2 < 0.01$, $P = 0.41$; both Poisson regressions; Fig. 2). Mean and *SD* of all embryo counts was 4.83 ± 1.29 (Fig. 3), with a total range of 1–10 (Figs. 2 and 3). The distribution of litter sizes was nearly symmetric, with skewness of only 1.92×10^{-3}.

Visual examination of residual and Q–Q plots for standardized residual range and normality suggested adequate model fitting for our litter size–climate models. However, examination of condition indices and variance decomposition proportions for models that included HB showed evidence of collinearity (e.g., scaled conditions numbers > 30; Table 2). As a result of these unacceptable condition numbers, we do not discuss models containing HB any further.

The global model containing the eight climate variables (but not HB) was highly statistically significant ($R^2 = 0.10$, $P << 0.01$; Table 2; Supplementary Data SD5) and among the top two AIC-ranked models with acceptable condition numbers. That model recovered significant relationships of litter size with long-term average of number of frost-free days (NFFD) and short-term temperature and precipitation (TB, PB). The short-term proxy of day during frost-free period (DFFP) was marginally significant in this model ($P = 0.06$). There was no relationship between other long-term (TS, PS) or short-term (NFFD_anomaly, FDD_anomaly) variables and litter size in the global model. The ratio of residual deviance to degrees of freedom for the global model was 0.31, and we failed to reject our null hypothesis of equidispersion for the litter-size data ($Z = -54.84$, $P = 1$).

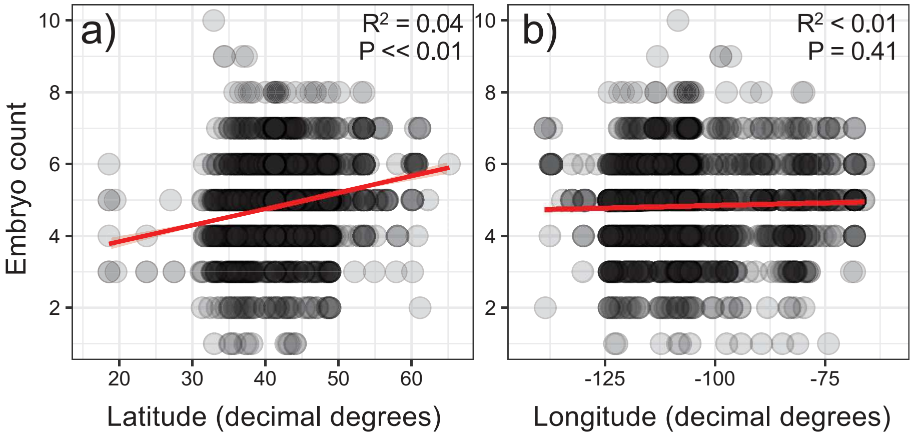

Fig. 2.—Relationship of *Peromyscus maniculatus* litter size with a) decimal latitude and b) decimal longitude. Results of Poisson regressions are listed as text on each plot. The best-fit line from a linear regression of the data is shown here to aid visualization (results were qualitatively similar to Poisson regressions).

However, the global model was indistinguishable from models containing long-term climate variables only, or long-term variables plus DFFP (ΔAIC scores of 0.1 and 1.9, respectively; Table 2). NFFD was the top predictor in all of these models, and in the global model had an effect size roughly twice the magnitude of any other significant variable based on the scaled predictor coefficients (Table 2; Supplementary Data SD5). Although the short-term temperature and precipitation variables (TB, PB) that we recovered as significant in the global model were also significant in models with only short-term climate variables, comparison of scaled effect sizes (Supplementary Data SD5) and correlation coefficients (Table 2) suggested that these short-term variables contain minimal predictive power.

Results of linear mixed models that incorporated a random effect for sampling bout (effectively, "site" × year) were highly consistent with those of general linear models (Supplementary

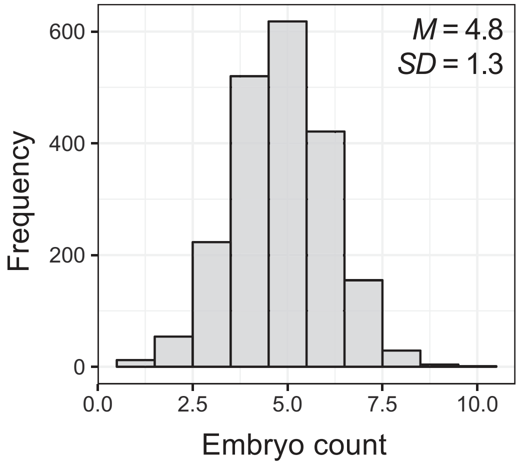

Fig. 3.—Distribution of *Peromyscus maniculatus* litter sizes contained in our data set. The mean and *SD* are listed at top right.

Table 2.—Summary of regression results relating litter size of *Peromyscus maniculatus* to predictor variables. Models are separated into those that include only climate variables (top) and those that include climate variables and head-body length (bottom), with ΔAIC calculated separately for the two model sets. Variable abbreviations correspond to Table 1. R^2 is the pseudo-R^2 of Zhang (2017). Embs = embryo counts. The preferred model (i.e., the model detailed in Table 3) is indicated by asterisks.

Model	Significant variables (and direction)	R^2	*P*	*d.f.*	Condition number	ΔAIC
Climate variables only						
**Embs ~ TS + PS + NFFD + TB + PB + NFFD_anomaly + FDD_anomaly + DFFP	NFFD (–), TB (–), PB (–)	0.10	<< 0.01	2,035	27.79	0.1
Embs ~ TS + PS + NFFD	NFFD (–)	0.09	<< 0.01	2,035	21.90	0
Embs ~ TS + PS + NFFD + DFFP	NFFD (–)	0.09	<< 0.01	2,035	23.07	2.0
Embs ~ TB + PB + NFFD_anomaly + FDD_anomaly	TB (–), PB (–)	0.02	<< 0.01	2,035	6.04	46.9
Embs ~ TB + PB + NFFD_anomaly + FDD_anomaly + DFFP	TB (–)	0.02	<< 0.01	2,035	8.30	48.7
Climate and phenotypic variables						
Embs ~ TS + PS + NFFD + TB + PB + NFFD_anomaly + FDD_anomaly + DFFP + HB	NFFD (–), TB (–), DFFP (+), HB (+)	0.21	<< 0.01	1,852	50.55	0.1
Embs ~ TS + PS + NFFD + HB	NFFD (–), HB (+)	0.20	<< 0.01	1,852	42.05	0
Embs ~ TB + PB + NFFD_anomaly + FDD_anomaly + HB	TB (–), HB (+)	0.14	<< 0.01	1,852	32.46	43.1

Data SD6). As above, the top three AIC-ranked models were the global model and models containing long-term climate variables only, or long-term variables plus DFFP (ΔAIC scores of 0.1 and 1.8, respectively; Supplementary Data SD6). Across all mixed models, the random effects explained negligible amounts of variation, which suggested that among-bout variation in litter size is extremely low relative to total range-wide variation.

Variation in litter size followed broad continental trends in NFFD, which was expected given the predictive power of that variable (Fig. 4). Thus, range-wide variation in *P. maniculatus* litter size can be characterized as exhibiting a broad latitudinal gradient overlain with significant variability at zones of known heterogeneity in frost-free season lengths. Across large parts of the eastern and central United States, as well as parts of southern Canada, where lengths of the frost-free period are similar, clines in litter size are gradual. Conversely, steeper clines in litter size occur where climate regimes change more abruptly, such as across the Rocky Mountain cordillera and along the transition from the Sierra and Cascade ranges to the Pacific Coast. Litter-size variation is therefore unevenly distributed across the geographic range of *P. maniculatus*. It is particularly notable that the full range of NFFD categories (and, thus, a large range of litter sizes) can be found in some narrowly defined geographic regions, such as the southwestern United States and southern California (Fig. 4).

When we examined variation in the phenotypic metric (HB) itself outside of climate models, we found highly significant negative relationships between HB and both NFFD and DFFP ($P < 0.01$ for both). This suggested that larger-bodied (and presumably older) females contribute more early season litters and smaller-bodied females contribute more late season litters across the range of *P. maniculatus* ($R^2 = 0.03$, *d.f.* = 1,849, $P << 0.01$ for the full model). The model also recovered a highly significant positive interaction between NFFD and DFFP ($P < 0.01$), indicating that the above demographic trend becomes more pronounced as the frost-free period gets shorter. Separate linear regressions of HB on DFFP within each NFFD quartile (Table 3; Fig. 5) revealed that the intra-annual decrease in body size is statistically driven by trends in the bottom two NFFD quartiles (i.e., areas with 62–177 frost-free days); the slopes of these regressions became steeper when we only considered records occurring on or after the first frost-free day (Table 4). However, we also detected a significant decrease in maternal body size within the top NFFD quartile when considering only records from within the frost-free period (215–365 frost-free days; Table 3; Fig. 5).

Impacts of age-structured breeding on litter size were borne out statistically only in the most extreme NFFD bins. For regions with highest seasonality (62–147 frost-free days), where maternal body size decreases most across the breeding season, a significant negative relationship existed between litter size and DFFP ($Z = -2.08$, $P = 0.03$) but not maternal body size ($Z = 0.97$, $P = 0.33$). This suggested that decreases in litter size that occur across the breeding season in these areas are due to factors other than the decreasing body size of breeding females, possibly their decreasing age or parity. Conversely, in the most aseasonal regions (215–365 frost-free days), litter size was positively correlated with maternal body size ($Z = 3.22$, $P < 0.01$) but not DFFP ($Z = 0.87$, $P = 0.38$). Thus, body size was a more reliable predictor of litter size in aseasonal areas, possibly because young-of-year females can delay reproduction longer than in more seasonal regions. However, the lack of a correlation between litter size and DFFP in aseasonal areas may have also been due to more complex phenologies in aseasonal regions (e.g., winter breeding seasons—Bronson 1985; Millar 1989).

Regression of litter size on 20-year time bins, while also accounting for effects of NFFD and the known temporal changes in NFFD during this time, revealed a statistically significant negative shift in litter size (Table 4). All three terms were statistically significant in our model. In addition, a complimentary regression of litter size on NFFD regime (i.e., pre- or post-1980, instead of smaller 20-year bins) was highly significant ($R^2 = 0.08$, *d.f.* = 2,035, $P << 0.01$), with all three terms achieving statistical significance. The direction of the litter-size change in both models (inversely associated with NFFD regime) is consistent with

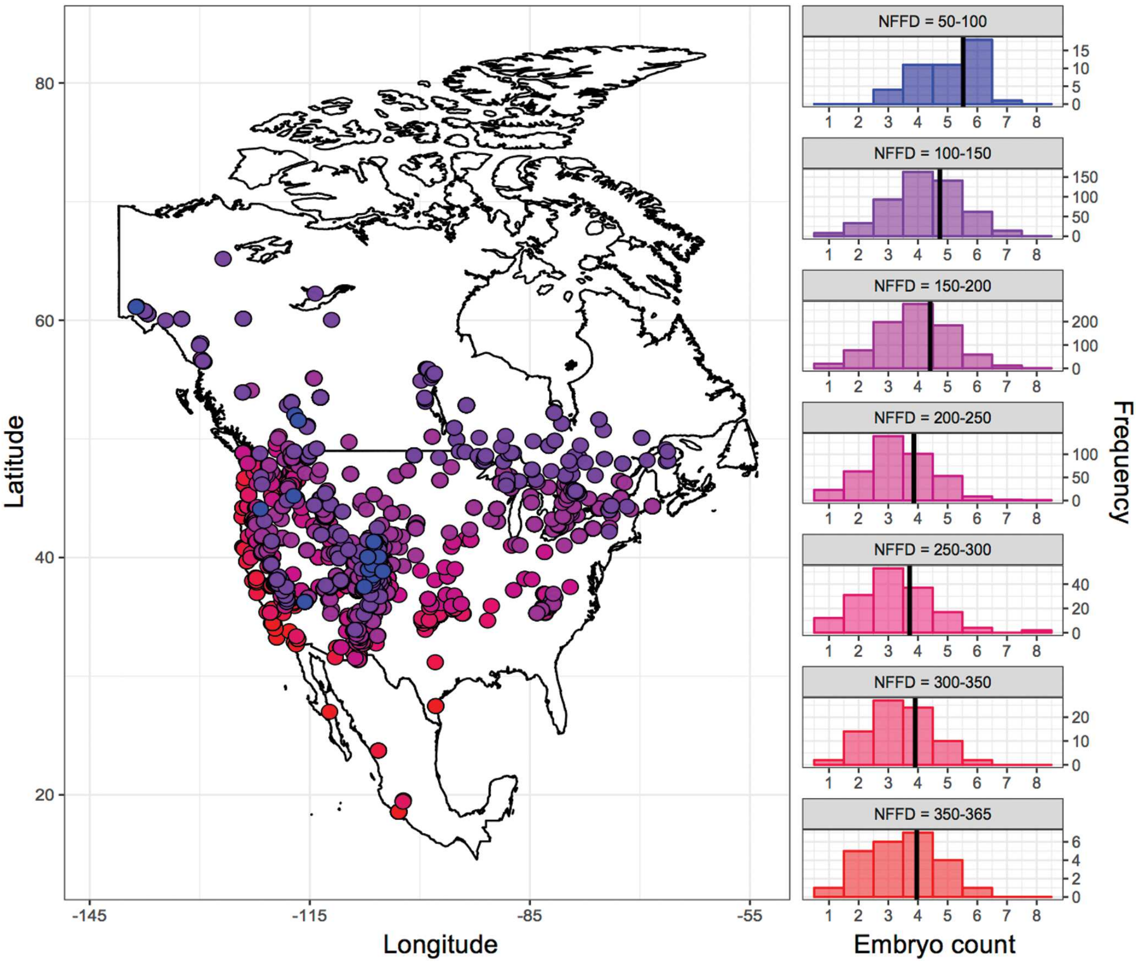

Fig. 4.—Geographic distribution of *Peromyscus maniculatus* litter-size records binned and colored by long-term number of frost-free days (NFFD). Records from areas with shortest and longest frost-free periods are in blue and red, respectively. Histograms in the right panel show the distribution of all litter sizes (colored bars) as well as the mean litter size (black line) within each NFFD bin. Litter-size records greater than eight were omitted from several histograms for clarity but are shown in Fig. 2.

Table 3.—Relationship of *Peromyscus maniculatus* maternal body size (HB) with day during frost-free period (DFFP) in different frost-free day zones. Embryo counts were binned by the long-term average number of frost-free days (NFFD). Within each of the NFFD quartiles, separate regressions were run using all records (upper rows) or only records occurring on or after the first frost-free day (i.e., DFFP ≥ 0; lower rows). Statistically significant regressions are indicated in bold.

NFFD quartile	Number of frost-free days for records in quartile	Slope for DFFP term	*t*-value for DFFP term	R^2	*P*	*d.f.*
1	62–147	−0.042	−4.436	0.039	**< 0.01**	453
		−0.060	−4.475	0.056	**< 0.01**	315
2	148–177	−0.029	−3.599	0.025	**< 0.01**	462
		−0.040	−3.078	0.025	**< 0.01**	327
3	178–214	−0.007	−1.246	0.001	0.21	462
		−0.018	−1.764	0.005	0.07	363
4	215–365	−0.001	−0.427	−0.001	0.66	468
		−0.014	−2.367	0.012	**0.01**	365

theoretical expectations if lengthening frost-free periods are resulting in a longer breeding season, and therefore more lifetime breeding attempts, for *P. maniculatus*. When we performed independent regressions of litter size on NFFD regime within NFFD quartiles (effectively modeling temporal trends within broad climatic zones), no significant correlations were recovered in any single NFFD group, although the effect of NFFD regime was marginally significant in the lowest NFFD bin (i.e., areas with shortest frost-free periods; $R^2 = 0.03$, *d.f.* = 508, $P << 0.01$, for the full model). We note that all of these results should be interpreted with caution given the smaller effect size of time bin (or NFFD regime) in the model relative to NFFD. Additional caution is warranted given that spatial sampling (based on latitude and longitude) was heterogeneous through time in our data set, although we did not detect significant differences

Table 4.—Trends in *Peromyscus maniculatus* litter size through time in our sample. Qualitatively similar model results were obtained when embryo counts were binned into broader frost-free period regimes (pre-1980, post-1980).

Model variable	Estimate	*Z*	*P*
Intercept	2.078	18.499	**<< 0.01**
Number of frost-free days (NFFD)	−21.971	−4.312	**<< 0.01**
20-year time bin	−0.057	−2.282	**0.022**
NFFD × 20-year time bin	2.278	2.005	**0.045**
P	**<< 0.01**		
R^2	0.088		
d.f.	2,035		

among temporal quartiles in mean NFFD (Supplementary Data SD3 and SD4).

Discussion

Climate controls on Peromyscus *litter size.*—The tendency for core life history traits to vary over broad climate and environmental gradients is apparent within many vertebrate groups (Lack 1947; Lord 1960; Cardillo 2002; Jetz et al. 2008; Tökölyi et al. 2014). Contextualizing this variation with respect to potential drivers, however, can be challenging. That often has been the case in mice of the genus *Peromyscus*, which are common and widespread components of North American mammal communities. Although *Peromyscus* energetics and life history were studied extensively in laboratory settings (e.g., Layne 1968; Drickamer and Vestal 1973; Modi 1984; Glazier 1985), a number of authors have been unable to consistently link reproductive traits of wild *P. maniculatus* populations (e.g., length of breeding season, timing of breeding, or litter size) to environmental and ecological variables (Glazier 1985; Bronson and Perrigo 1987; Millar 1989; Kalcounis-Rueppell et al. 2002; Millar and Herdman 2004). The latter results have been interpreted by some to result from a high degree of phenotypic (Layne 1968; Millar 1989) or behavioral (Bronson and Perrigo 1987; Kalcounis-Rueppell et al. 2002) plasticity in this species or, alternatively, evolutionary constraints on the particular life history traits under study (Millar 1982, 1989).

Our reevaluation of variation in litter size in *P. maniculatus*, the most geographically widespread species of deer mouse, provides several methodological advantages over previous range-wide studies of wild *Peromyscus*. First, use of morphological and life history trait data (i.e., embryo counts and body sizes) collected at the individual level precludes the need to rely on population averages; the latter approach can dampen statistical signal, particularly in discrete traits constrained to narrow ranges of variation (e.g., litter size). Use of individual-level data also allowed us to focus solely on intraspecific litter-size dynamics, in contrast to past studies that often conflated these with patterns at interspecific scales (i.e., across multiple species of *Peromyscus*). Second, use of historic climate data for the time and place of individual capture increased the spatiotemporal resolution of our predictor variables, allowing us to test links between intraspecific litter size and climate with higher precision, as well as to better contrast relative effects of short- and longer-term climate factors. Third, by leveraging the broad spatial and temporal sampling (greater than 100 years) represented by museum specimens, we greatly expanded the number of observations in our data set relative to previous studies. This improved statistical power via increased sample size, while also buffering the short-term climate stochasticities that potentially complicate shorter-term, population-level studies.

We found number of frost-free days (NFFD) to be the strongest predictor of range-wide variation in litter size in *P. maniculatus* (Table 2; Fig. 4). NFFD consistently emerged as a significant predictor across global models, as well as across submodels that included only long-term variables (Table 2; Supplemental Data SD5 and SD6). Conversely, metrics of short-term climate variability (e.g., temperature or precipitation seasonality, anomalies in NFFD or FDD) did a poor job of explaining variation in litter size (Table 2; Supplementary Data SD5 and SD6). Our recovery of persistent correlations between NFFD and litter size is in agreement with the more limited analysis of McLaren and Kirkland (1979), who found evidence for this same relationship in *P. maniculatus* across the central Appalachian region. Dunmire (1960) and Spencer and Steinhoff (1968) also regarded season length to be a major driver of litter-size variation in *P. maniculatus* along elevational gradients in California and Colorado, respectively.

Our results and those of the above studies strongly suggest that variation in litter size in *P. maniculatus* is partly an evolved response of populations to climatic or resource-driven constraints on the number of possible annual reproductive bouts. This finding is consistent with life history theory, which predicts that litter size should evolve to maximize lifetime reproductive fitness of females, which is shaped by constraints on the number of lifetime breeding opportunities. However, multiple mechanisms are capable of producing the correlations we observed. For example, highly seasonal (thus, low NFFD) areas may experience climatic or resource fluctuations that directly impact the number of successful breeding attempts via energetic limitations. Highly seasonal areas are also typically characterized by longer winters with more severe winter temperatures. Severe winters can reduce overwinter survival, leading to recurrently low population sizes in spring and selection for larger litters due to the higher resource availability and survival rates that these litters experience. These hypotheses are not mutually exclusive and testing each of them may require experimental manipulations of individuals or populations, or even transplant-based approaches.

Millar (1989) previously quantified range-wide litter size in *P. maniculatus*, but suggested that variation in this trait was uncorrelated with length of the breeding season (i.e., the annual duration of population reproductive activity). Therefore, Millar's (1989) findings are potentially inconsistent with theoretical expectations. Moreover, if we assume that numbers of breeding opportunities are related to the length of the frost-free period, his findings also seem to contradict studies linking litter size to season length (Dunmire 1960; Spencer and Steinhoff 1968; McLaren and Kirkland 1979; this study). Several methodological factors could explain these discordances. First, Millar's (1989) literature-derived data set was geographically coarser than our individual-based data set; this probably

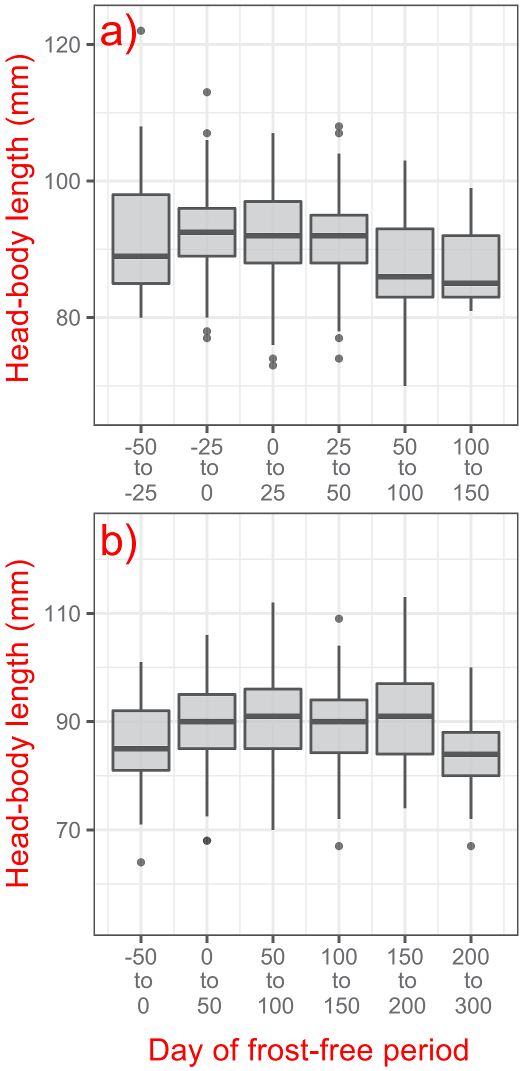

Fig. 5.—Annual body size trends of breeding female *Peromyscus maniculatus* for a) areas with the shortest frost-free seasons (i.e., lower NFFD quartile) and b) longest frost-free seasons (upper NFFD quartile). Body sizes are binned by Julian day since beginning of the frost-free period (the DFFP variable); note the size of bins varies between plots, reflecting the magnitude of difference in length of the frost-free period. Four records greater than 50 days before the frost-free period were omitted from a) for consistency with b).

blurred clines of litter-size variation across finer spatial (especially elevational) gradients. Second, Millar's (1989) data sets describing litter size and breeding-season length are from only partially overlapping groups of populations. Both factors limit the statistical robustness of that study. Our study demonstrates a strong correlation of litter size with NFFD, suggesting there is mechanistic link between the two factors, but establishing this link requires additional efforts to statistically associate NFFD (or some comparable metric of climatic seasonality) with actual breeding-season length in this species.

Despite the explanatory power of NFFD in our study, global models still accounted for a relatively small amount of overall variation in litter size. Previous workers, in attempting to explain patterns of variation in *P. maniculatus* litter size, suggested this trait may not actually be shaped by broad climate factors, but instead may represent responses to resource availability at local scales (Modi 1984; Glazier 1985; Millar 1989). In an attempt to address that hypothesis, we included instantaneous climate variables (monthly temperature and precipitation for the location of capture) in our models that should be at least partially predictive of local resource availability. These variables (TB, PB) added little predictive power, although they were statistically significant in the global model as well as in models with only short-term climate variables (Table 2; Supplementary Data SD5 and SD6). However, the direction of both relationships was negative (Table 2), which is counterintuitive because temperature and precipitation should partly modulate food resources (e.g., plant material, insects, or both) available for females to invest in production of offspring. One explanation for the generally low predictive power of short-term climate variables is that our climate data set is still temporally limited. Specifically, access to historical climate data at higher (e.g., daily or weekly) resolution might allow construction of more precise predictor variables and use of more powerful and temporally flexible statistical methods (e.g., sliding window analyses).

Temporal and demographic considerations.—Even in the case of more precise temporal analyses, short-term climate data alone may be insufficient for predicting actual resource availability at the place and time of capture. This is because *P. maniculatus* is an omnivore that consumes a diversity of seeds, grains, and acorns (Gashwiler 1979; Merritt and Merritt 1980; Ostfeld et al. 1996), and the peak availability of these resources lags peaks in primary productivity in some regions (e.g., Luis et al. 2010). Resource availability also can be modulated by population density, which is known to fluctuate significantly in *P. maniculatus* (Blair 1940; Beer and MacLeod 1966; Bradley and Mauer 1967; Sullivan 1977; Krebs and Wingate 1985; Wolff 1985; Drost and Fellers 1991; Calisher et al. 2005; Loehman et al. 2012; but see Terman 1966) and is itself subject to temporal lags (Luis et al. 2010). Accommodating complex dynamics such as these in life history analyses is extremely difficult because their presence and timing can vary among populations and geographic regions and be stochastic over short temporal scales (Kesner and Linzey 1997; Kalcounis-Rueppell et al. 2002; Millar and Herdman 2004; Calisher et al. 2005; Loehman et al. 2012). Also, it is possible that short-term resource availability modulates reproductive parameters besides litter size. For example, Gashwiler (1979) found no differences in litter sizes of *P. maniculatus* among good and poor seed years in western Oregon, but did observe changes in the relative number of breeding females as well as numbers of litters produced annually. As these dynamics suggest, a more complete understanding of the evolution of litter size in *P. maniculatus* and other small mammals will depend not just on more precise climate data, but also on the ability to integrate relevant primary productivity metrics or population-level variables into future analyses.

Nevertheless, we did recover known demographic patterns across large geographic scales using our existing data set. Populations of *P. maniculatus* in highly seasonal environments tend to display age-structured breeding, with the oldest adults contributing more litters early in the season, and younger age cohorts contributing more litters later in the season (Coventry 1937; Blair 1940; Dunmire 1960; Sheppe 1963; Vaughan 1969; Gashwiler 1979; Millar et al. 1979) or, alternatively, postponing breeding until the following spring (Dunmire 1960; Sheppe 1963; Brown 1966; Millar and Innes 1983; Wolff 1985). Our models confirmed intra-annual decreases in maternal body size across the year, as well as a strengthening of this effect with increasing seasonality (and decreasing NFFD; Table 3). However, we found little evidence that those changes in female body size constitute proximate controls on litter size; we only detected a significant effect of HB on litter size in the most aseasonal environments (Supplementary Data SD7). Previous authors also recovered mixed support for a relationship between litter size and maternal body size within populations (Rolan and Gier 1967; Myers and Master 1983; Millar 1985). Our results may reflect the stricter trade-offs that exist between body condition and breeding in highly seasonal environments, where a higher proportion of females must breed simultaneously regardless of body size or condition. It is also possible that litter size varies more strongly with parity than with body size across the range of *P. maniculatus*, as was evident in some previous population-level studies (Beer et al. 1957; Rolan and Gier 1967; Drickamer and Vestal 1973; Millar 1982; Myers and Master 1983). All of these dynamics are nonlinear and difficult to account for in our data set, and future studies would benefit from more precise information on female age and parity (e.g., using other external phenotypic metrics or possibly skeletal indicators to assign ages).

Life history response in an era of global change.—Life history responses to recent climate changes have been documented in several North American mammal species to date (e.g., *Marmota flaviventris* in Colorado—Inouye et al. 2000; Ozgul et al. 2010; *Urocitellus columbianus* in Alberta, Canada—Lane et al. 2012; *Tamaisciurus hudsonicus* in Yukon, Canada—Réale et al. 2003, but see Lane et al. 2018). However, the taxonomic and geographic sparseness of these studies reiterates the need to develop long-term monitoring programs focused on easily trackable phenotypic and life history traits of small mammals (Kissling et al. 2018). *Peromyscus maniculatus* typically is considered a highly adaptable species due to its broad ecological tolerances and range-wide variability in physiological and life history traits. In areas of documented climate change (e.g., northern temperate latitudes or steep elevational gradients), it may be reasonable to expect some populations of *P. maniculatus* to have responded to climate changes in situ, via plasticity or microevolution in behavioral or physiological traits (sensu Boutin and Lane 2013).

The length of the frost-free period in parts of North America has increased by roughly 2 weeks since the late 19th century, with half of that change occurring since 1980 alone (Kunkel et al. 2004; Barichivich et al. 2012). After accounting for effects of NFFD (our strongest predictor) on litter size and the change in this parameter through time, we detected a statistically significant decrease in *P. maniculatus* litter size during the last century. Results were comparable whether observations of litter size were aggregated into 20-year bins ($n = 6$), or into known NFFD regimes ($n = 2$, pre- and post-1980). The direction of the shifts was consistent with expectations if NFFD has resulted in more annual breeding opportunities for some *P. maniculatus* populations. The potentially greater contribution of low-NFFD populations to this trend, although only marginally statistically significant, is also consistent with the relatively greater changes in frost-free period length that have occurred at higher latitudes (Barichivich et al. 2012). The overall variance explained by time bin (or NFFD regime) is relatively small, however, and we consider our results to be preliminary at best. Further work examining trends in NFFD and litter size through time, as well as the potential for sampling biases through time, is crucial to permit more robust conclusions about this potential response.

Even if our finding of decreasing litter size is supported under further scrutiny, additional challenges exist for identifying its mechanistic basis. McCabe et al. (2015) demonstrated that lengthening of the frost-free period has involved a shift to earlier last spring frosts as well as to later first autumn frosts, but there is significant spatial heterogeneity in relative contributions of these variables (Cayan et al. 2001; Kunkel et al. 2004; Barichivich et al. 2012). In many parts of the western United States and southern Canada, longer spring seasons have made a greater contribution to the lengthening frost-free period than have longer autumn seasons (Kunkel et al. 2004; Barichivich et al. 2012). That particular dynamic could lead to relative increases in the number of litters birthed by adult, overwintered, and potentially multiparous females early in the season in these highly seasonal regions, which could generate a trend like the one we observed and does not invoke any evolved physiological or genetic response. Indeed, our densest sampling was from these areas (Figs. 1 and 4), and later years tended to have relatively more samples from both lower latitudes and longitudes (Supplementary Data SD3 and SD4). Parsing temporal trends in litter size in a more rigorous way will require assembly of more geographically focused data sets complete with other life history trait data, which could help avoid potential spatial and seasonal biases inherent in opportunistically collected data sets such as ours.

In general, it is unknown whether litter size or some alternative reproductive trait(s) is more likely to exhibit responses to changing climates in deer mice. Indeed, few studies have focused on these species in the context of recent climate change. However, there is some evidence for climate-mediated responses in *P. maniculatus* populations from the Great Lakes region. Those areas, which are historically characterized by long, severe winters, have experienced reductions in the commonness and abundance of *P. maniculatus* and possible ecological replacement by the ecologically generalist white-footed mouse, *P. leucopus* (Long 1996; Myers et al. 2005, 2009; Roy-Dufresne et al. 2013). These patterns have been interpreted as resulting from the diminishing competitive advantage of *P. maniculatus* (which is better adapted to severe winters) in an era of warmer temperatures and earlier spring arrival (Myers et al. 2005). As in our study, additional field-based life history studies are necessary to identify the exact mechanistic basis behind these changes (Myers et al. 2005).

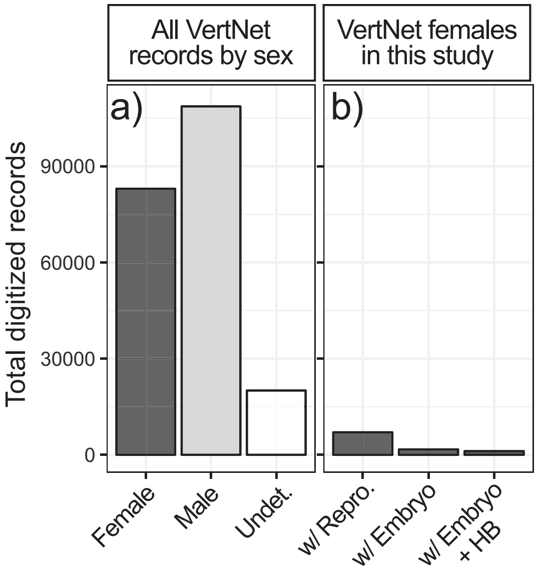

Fig. 6.—a) Records of *Peromyscus maniculatus* downloaded from VertNet for this study, plotted by sex (Undet. = sex unknown or ambiguous based on digital record). b) Records of female *P. maniculatus* in the same VertNet data set that contained matches to our broad reproductive terms, embryo counts specifically, or both embryo counts and external body measurement data. Both a) and b) are plotted on the same scale.

Digitized specimens and life history research.—Our work provides proof-of-concept for the utility of digitized natural history collections in providing the data on life history traits that are essential for global monitoring of mammal biodiversity (Kissling et al. 2018). In addition to representing data on spatiotemporal occurrence, museum specimens are a source of information on the diet, reproduction, genomes, and parasite communities of mammals that can inform a variety of ecological and evolutionary research questions (Suarez and Tsutsui 2004; Dunnum and Cook 2012; McLean et al. 2016; Cook et al. 2017; Schindel and Cook 2018). Significant progress has been made in the digitization and mobilization of mammal specimen records (Dunnum et al. 2018), but we are still in the early stages of aggregating and serving the true breadth of specimen-associated data in standardized digital formats (Ariño 2010).

Our study relied on just two basic measurements from georeferenced specimens (embryo counts and head-body lengths), but we encountered significant gaps in availability of these data within digitized specimen records (Fig. 6). Of the roughly 82,972 VertNet records of female *P. maniculatus* used in our study, only 8% (6,601) contained unambiguous matches to our broad reproductive search terms, 2% (1,671) contained embryo counts specifically, and 1.3% (1,132) contained both embryo counts and body length measurements and thus were immediately usable in our analyses. As a result, the total number of records we were able to leverage in our analysis is a small fraction of the information potentially archived in natural history collections.

Despite these small proportions, we observed a statistically significant increase in the proportion of VertNet records with associated embryo count data through time ($R^2 = 0.46$, $P << 0.01$ for a linear regression of log-transformed proportion of total VertNet females on year; Fig. 7). This trend is opposite to the general decrease in temporal representation of *P. maniculatus* specimens in collections over that same time period and a similar trend across North American mammals in general (Malaney and Cook 2018). Increases in the relative proportion of standardized and extractable digital reproductive data, although still less than 5% of specimens annually, may reflect a tendency of recent mammal collectors to capture more and varied types of data from specimens, and an increasing awareness of the value of digitizing these data by museums. Even if older specimens host proportionately less reproductive data (due to failure to record such data), historic collections likely still host a substantial amount of untapped information on species phenotypic and phenological traits that can be accessed at the individual level. Digitization of specimen data in richer detail, combined with new techniques to extract and expose these data (e.g., body mass and length—Guralnick et al. 2016), is critical to fuel new and innovative questions in mammalian life history biology, especially those focused on deciphering responses to global change.

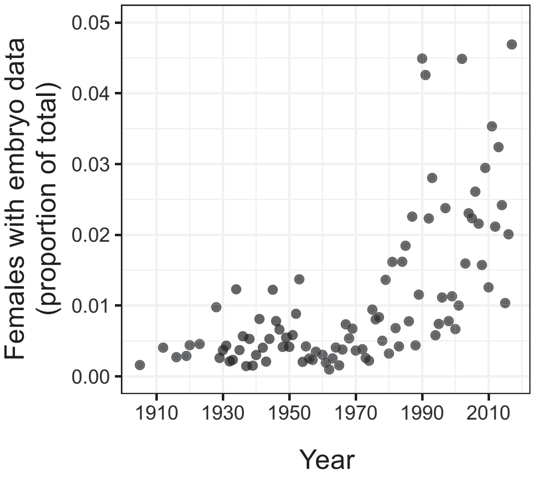

Fig. 7.—Proportion of *Peromyscus maniculatus* records downloaded from VertNet for this study for which embryo counts were detected, plotted against year of specimen collection. Years represented by only one specimen were omitted for clarity.

Acknowledgments

First and foremost, we thank the many collectors of primary mammalian trait data (museum specimens and census records) on whose work this paper is wholly based. We also thank J. Dunnum (MSB), J. Dines (LACM), B. Hess (NCSM), and B. Lim (ROM) for providing additional body measurements from specimens in their care. B. Stucky (FLMNH) provided access to R code for collinearity diagnostics of linear models. This work was supported by the NSF Postdoctoral Research Fellowship in Biology under grant no. 1812152 (BSM) and a University of Florida University Scholars Program award (JF).

Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Raw data used in this study including embryo counts, total, tail, and head-body lengths, collection dates, geocoordinates, raw and scaled (".cs") ClimateNA model variables, and additional derived model variables.

Supplementary Data SD2.—Day-of-year distributions of embryo count records.

Supplementary Data SD3.—Coarse spatial and temporal distributions of embryo count records.

Supplementary Data SD4.—Statistical properties of the embryo count data set across spatial, temporal, and climatic gradients.

Supplementary Data SD5.—Summaries of general linear models of litter-size variation.

Supplementary Data SD6.—Summaries of linear mixed models of litter-size variation.

Supplementary Data SD7.—Summaries of general linear models of maternal body size and litter-size variation.

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