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Red squirrel gestation length is unchanged by maternal traits, litter composition, or future food availability

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Abstract

Despite considerable research on reproductive timing, factors influencing intraspecific variation in gestation length in wild mammals have received limited attention, largely due to a lack of high-resolution data. We examined potential drivers of gestation length variation in a wild population of North American red squirrels (*Tamiasciurus hudsonicus* Erxleben, 1777) in Yukon, Canada. Drawing on 27 years of conception and parturition data, we found that gestation length was highly conserved, with minimal variation (35.4 ± 1.49 days; mean ± standard deviation). Gestation length was unaffected by maternal age, litter size, or litter sex ratio. Likewise, the anticipation of an upcoming food pulse, caused by synchronous conifer seed masting, had no statistically significant influence on gestation length. This finding stands in contrast to other reproductive traits in red squirrels, which are known to shift in response to food pulses. Overall, our results suggest that gestation length in red squirrels is buffered against environmental variability, likely due to stabilizing selection or strong heritability.

Key words: fitness, life-history, investment, offspring, reproduction, rodent

Résumé

Malgré les nombreuses études sur le calendrier de la reproduction, les facteurs influençant la variation intraspécifique de la durée de gestation chez les mammifères ont reçu peu d'attention, en grande partie en raison du manque de données à haute résolution. Nous avons examiné les facteurs potentiels pouvant expliquer la variation de la durée de gestation dans une population d'écureuils roux nord-américains (*Tamiasciurus hudsonicus* Erxleben, 1777) au Yukon, Canada. À partir de 27 années de données sur les conceptions et les mises bas, nous avons constaté que la durée de gestation était hautement conservée, avec très peu de variation (35,4 ± 1,49 jours; moyenne ± écart-type). La durée de gestation n'était pas influencée par l'âge de la mère, la taille de la portée, ou le ratio des sexes. De même, l'anticipation d'un pic alimentaire à venir, causé par une surproduction synchronisée de graines de conifères, n'avait aucun effet statistiquement significatif sur la durée de gestation. Ce résultat contraste avec d'autres traits reproducteurs chez l'écureuil roux, qui sont connus pour réagir aux pics alimentaires. Dans l'ensemble, nos résultats suggèrent que la durée de gestation chez l'écureuil roux est insensible aux fluctuations environnementales, probablement en raison d'une sélection stabilisatrice ou d'une forte héritabilité. *[Ceci est une traduction fournie par l'auteur du résumé en anglais.]*

Mots-clés : histoire de vie, investissement, progéniture, reproduction, ressource, rongeur

Introduction

Gestation must be completed successfully if a female mammal is to have any reproductive success, making length of the gestational period a key component of mammalian reproduction. Gestation length has been widely studied in domestic mammals (e.g., Kennedy and Moxley 1978; Foote 1981; Heck et al. 2017) due to its economic value in predicting birth dates and managing parturition (Bourdon and Brinks 1982). However, in wild populations, tracking exact conception dates is difficult (Berger 1992; Clements et al. 2010), and reliably monitoring females poses additional challenges, making gestation length rarely documented in wild mammals. Across a broad range of species, detectable patterns exist between estimated gestation length and other mammalian life history traits, such as body size and lifespan (Danis and Rokas 2024). However, the factors influencing variation in gestation length within species have received comparatively less attention in studies of life history evolution.

While gestation is only one component of the reproductive period in mammals, it plays a critical role in shaping offspring development before birth. Some authors have argued that lactation is more energetically demanding than gestation, particularly in small mammals (Gittleman and Thompson 1988; Kenagy et al. 1989). However, gestation represents the non-negotiable minimum maternal investment—completion is essential for reproductive success (Bronson 1989). Unlike lactation, gestation length in wild populations is a tightly regulated and conserved phase within species (Michener 1980; Holand et al. 2005), although some variability exists (e.g., Racey 1981; Weller et al. 2023). Gestation variation is especially true for heterothermic bats that use torpor in response to adverse conditions (Fjelldal and van der Kooij 2024; Zukal et al. 2024). Intraspecific variation in gestation length, when present, is often linked to specific biological factors. Reproductive senescence, or age-related changes, can influence gestation length, with older females often having longer pregnancies (Emlen 1970; Lemaître et al. 2020). Younger females may also experience longer gestation as they balance trade-offs between growth and reproduction (Descamps et al. 2007). In species with multiple offspring, gestation length may increase with larger litters (Huber et al. 2001) or male-biased litters due to the higher energetic demands of male offspring (sensu Clutton-Brock et al. 1982; Mysterud et al. 2009). Similar to other reproductive traits (Kiltie 1982), gestation length can fluctuate with food availability, as seen in white-tailed deer (*Odocoileus virginianus* Gmelin, 1877; Verme 1965), horses (*Equus caballus* Linnaeus, 1758; Howell and Rollins 1951), and sheep (*Ovis aries* Linnaeus, 1758; Alexander 1956). Variation in gestation length may serve as an adaptive mechanism to optimize offspring survival in changing environments. Few hypotheses address the causes of variation in gestation length in wild mammals. One hypothesis suggests that gestation in large, gregarious mammals may be shortened and synchronized when maternal body condition is good (Berger 1992). However, hypotheses specifically addressing small mammals are nonexistent.

Here we focus on gestation length as a key axis of maternal investment and reproductive timing in a small wild mammal, North American red squirrels (*Tamiasciurus hudsonicus* Erxleben, 1777); hereafter "red squirrels". We used data spanning 27 years from a population in Yukon, Canada. Red squirrels are an ideal species to study gestation because we are able to monitor pregnancies from conception through parturition with high resolution, while tracking the local conditions experienced by females during this time on their 0.2–0.5 ha territories (Price et al. 1986).

Red squirrels have a relatively long lifespan when compared to other small rodents (3.53 ± 0.13 years (mean ± standard deviation (SD)), median 3.5 years, maximum of 9 years (McAdam et al. 2007; Petrullo et al. 2024)). Females can breed up to age 7 years (Descamps et al. 2008). However, after age 5 years, red squirrels experience the most intense effects of senescence, which affect many traits, including reproduction, body mass, and food cache size (Descamps et al. 2007, 2008; Wishart 2023). In our study population, mating typically commences in late January to mid-February (Lane et al. 2007), although females can enter oestrus as late as April or May (Dantzer et al. 2020). On average, females have 3.02 ± 0.71 offspring per litter (McAdam et al. 2007). Historically, gestation length was estimated to be 40 days in this species, based on the assumption that it would be shorter than the 44-day average for the larger gray squirrel (*Sciurus carolinensis* Linnaeus, 1766; Hamilton 1939). Published estimates from both wild and captive populations place gestation length between 31 and 35 days (Prescott and Ferron 1978; Lair 1985). Subsequent studies, including ours, have used 35 days as the standard estimate (e.g., Lane et al. 2008, 2009).

Red squirrel reproductive timing is closely linked to the cone masting of white spruce (*Picea glauca* (Moench) Voss; Williams et al. 2014), a synchronised but irregular process characterised by the production of large quantities of seeds (Nienstaedt and Zasada 1990). White spruce cone maturation occurs in the autumn, triggering red squirrels to engage in intensive collection of these cones, their primary food source (Fletcher et al. 2010). Years of high cone production, crucial for building food caches, are interspersed with periods of low cone yields, making red squirrels heavily reliant on the reserves stored during previous spruce mast years (Haines et al. 2022). In anticipation of an autumn spruce mast, selection favours increased reproductive output by female red squirrels; larger litters are seen, second litters may be attempted, and more yearling females breed (Boutin et al. 2006; McAdam et al. 2019; Petrullo et al. 2023). Given the documented variation in gestation length in this species (range = 29–39 days, see results), we hypothesized that reducing gestation length during spruce mast years might serve as a mechanism to increase offspring production. For instance, females can be both pregnant and lactating at the same time in mast years, as seen in offspring overlap of both the North American red squirrel (Boutin et al. 2006; McAdam et al. 2007) and the European red squirrel (*Sciurus vulgaris* Linnaeus, 1758; Selonen et al. 2015). Shortening the gestation period could lead to a shorter inter-birth interval, as in wild chimpanzees (Feldblum et al. 2022). Second litters do pose challenges because females must balance lactation with caching of spruce cones late in the season (Archibald 2011). A shorter gestation period would minimize this overlap.

Given this natural history, our objective was to identify the factors driving variation in gestation length in female red squirrels. Based on empirical evidence from other species, we predicted a longer gestation when females: (1) were younger or older (e.g., Emlen 1970; Lemaître et al. 2020); (2) had larger litters (e.g., Huber et al. 2001); (3) produced male-biased litters (sensu Clutton-Brock et al. 1982; Mysterud et al. 2009); or (4) conceived in a nonspruce mast year (sensu Boutin et al. 2006; Williams et al. 2014; McAdam et al. 2019; Petrullo et al. 2023).

Materials and methods

Ethics statement

This project was approved by the University of Alberta (Animal Care Permit AUP000000028) and the Yukon Government's Department of Tourism and Culture (Yukon Science and Explorers Permit 23-05S&E, 22-08S&E, 22-07S&E, 21-16S&E, 21-11S&E, 20-11S&E, 19-06S&E, 18-08S&E, 17-13S&E, 16-09S&E, 15-07S&E, 14-07S&E, 13-09S&E, 12-09S&E, 11-04S&E, 10-06S&E, 09-09S&E, 08-03S&E) and Department of Environment (Wildlife Research Permit 368).

Study area

We collected data from seven study areas near Kluane Lake (61°N, 138°W) in Yukon, Canada, between 1995 and 2022. To maximise sample size, we included gestation length data from both control and experimentally manipulated study areas. Three study areas were part of food addition experiments conducted between 2004–2017, 2005–2011, and 2006–2012. Between 2015 and 2022, data also included experimental glucocorticoid manipulations at two study areas. Over our study period, six spruce mast events occurred, on average every 4.8 ± 1.3 years.

Data collection

We monitored a population of individually marked-female red squirrels. Most individuals were tagged as juveniles in their natal nests with permanent alphanumeric ear tags and visual markers; immigrants were captured and tagged upon arrival. We assumed unknown-age females were yearlings based on body mass and nipple condition (Lane et al. 2010; Martinig et al. 2020; full details in Supplementary Material). We tracked females across the full gestational period by maintaining a fully enumerated population and conducting biannual censuses to monitor territory ownership, survival, and reproductive status (Dantzer et al. 2020; Martinig et al. 2020).

Female red squirrels enter oestrus for ~1 day during late winter (Lane et al. 2007), and we recorded mating dates based on observed copulations or mating chases. Opportunistic observations occurred throughout the study, and we conducted systematic monitoring in 2003–2005 and 2008. We inferred copulations based on vocalisations and underground pairing durations (≥60 s; Lane et al. 2008; see Supplement Material for protocols across years). To estimate gestation length, we backdated birth dates based on pup mass at first nest entry (McAdam et al. 2002) and determined the gestation period by subtracting the mating chase date (i.e., date of conception) from the birth date, to the nearest day. This adjustment likely reduced variation in gestation length estimates by standardising the estimation of birth dates across individuals. Without this adjustment, differences in the timing of first nest entry (e.g., if pups were first observed at 2 vs. 5 days old) would introduce additional noise, inflating the variance in gestation estimates due to inconsistent observational lag rather than biological differences. Thus, the backdating procedure improves comparability and precision in estimated gestation lengths. At first nest entry, we recorded litter size, sex, and pup mass, and used these data to calculate sex ratios.

Data analysis

We analysed gestation length (in days) using a Gaussian linear regression. Our final dataset included 174 litters from 160 females with observed mating chases. To account for among-year variation not explained by measured covariates and the nonindependence of repeated measurements of females, we included year and maternal identity, respectively, as random effects. We included maternal age (both linear and quadratic terms to capture potential nonlinear effects), litter size, litter sex ratio, and their interaction as fixed effects. Although the linear and quadratic terms for age were highly correlated (as expected for polynomial terms) multicollinearity was assessed and found to be negligible (see Supplemental Materials). We also included treatment group (control, experimental, or food-supplemented), cone abundance from the previous autumn (see Supplemental Material for detailed methodology), and whether the pregnancy occurred prior to a spruce mast (1 = spruce mast in autumn and 0 = no spruce mast in autumn), as fixed effects. We mean-centred and standardised numerical predictors within study area and year to facilitate interpretation. We report means ± SD throughout unless otherwise noted. We conducted all analyses in R, version 4.2.0 (R Development Core Team 2024; see Supplementary Material for packages and full model details). We provide additional information on model interpretations, standardisation procedures, and collinearity assessments in Supplemental Material.

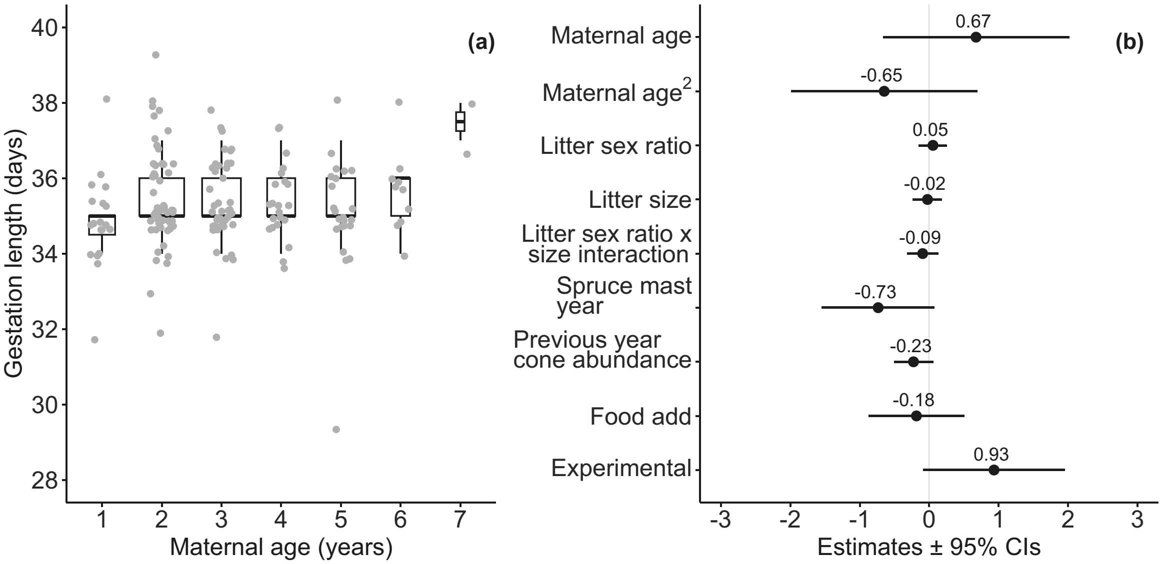
Results

Females had a mean gestation length of 35.4 ± 1.5 days (median = 35, range = 29–39, $n = 160$ females and 174 litters). Maternal age did not significantly affect gestation length (Fig. 1*a*; Table S1), although yearling females had the shortest mean gestation length (34.9 ± 1.18 days; $n = 19$ females and 19 litters). Females between 2 and 6 years old had similar gestation lengths, with an overall mean of 35.4 ± 1.2 days. The longest gestation lengths in our dataset were recorded for the two 7-year-old females (37 and 38 days; $n = 2$ litters). Litter size and composition (including the interaction term), experimental manipulations, previous year's cone abundance, and the occurrence of an upcoming spruce mast, had no significant effect on gestation length (Fig. 1*b*; Table S1). The marginal R^2 was 0.12 and the conditional R^2 was 0.34.

Discussion

Quantifying gestation length in wild populations is challenging due to the need for precise conception dates (Clements et al. 2010) and detailed monitoring of known individuals. Consistent with findings in other species (Michener 1980; Holand et al. 2005), we found that red squirrels exhibit relatively invariable gestation lengths, although a few cases resulted in a large range around the mean. Maternal age, litter size, litter sex ratio, previous or upcoming cone

Fig. 1. (*a*) Sources of variation in gestation length (days; $n = 160$ females and 174 litters) for female North American red squirrels. We mean-centred and standardised variables within study area and year prior to analysis. Numbers above estimates are point estimates from a linear regression model (Gaussian with identity link) for fixed effects with bars indicating 95% confidence intervals (CIs). We present full results in Table S1. (*b*) Gestation length (days) did not significantly change with maternal age (years).



abundance, and experimental manipulations had no significant impact on gestation length.

Low variability in gestation length is common among wild mammals (Michener 1980; Holand et al. 2005; but see Racey (1981) regarding bats), and is considered a robust feature of mammalian reproduction (Asher 2007). Although we are not aware of any evidence for delayed implantation in red squirrels, this mechanism, observed in species such as mustelids, can offer reproductive timing flexibility and may help explain gestation variation in other taxa (Sandell 1990). For females, the physiological costs of reproduction, including impacts on survival and longevity (Millar 1977), make consistent gestation periods advantageous by reducing negative cascading effects on life history timing. Resource trade-offs among gestation, lactation, and rearing are finely tuned to optimize both maternal and offspring survival. In red squirrels, female survival is positively correlated with population growth (McAdam et al. 2007), and changes in reproductive traits, particularly those tied to generation time, can influence population dynamics (Gaillard et al. 2005). As such, stabilizing selection likely acts strongly on gestation length, maintaining it near an optimal duration for the species. The limited intraspecific variation observed in red squirrels suggests that gestation length is a highly conserved trait (Asher 2007), linked to both reproductive success and offspring viability (Danis and Rokas 2024).

Although adequate female body condition is one of the few physiological requirements for pregnancy in many species (Clauss et al. 2021), red squirrels rely on multiple food sources to sustain reproduction (Fletcher et al. 2013). Ecologically, red squirrels function as capital breeders, accumulating energy in advance of reproduction. Yet, physiologically, they behave more like income breeders, drawing from their cache to fuel reproduction. During nonspruce mast years, red squirrels survive by combining stored resources from previous spruce mast events with newly acquired food (Dantzer et al. 2020). Despite this reliance on cached resources, cache size does not influence body mass (Wishart 2023), suggesting a resource budgeting strategy that explains the lack of detectable effects of resource abundance, whether past or present, on gestation length. While interannual variation in regional food abundance has population-wide effects (McAdam and Boutin 2003; Boutin et al. 2006; Williams et al. 2014; Dantzer et al. 2020, 2022; Petrullo et al. 2023), it does not appear to extend to gestation length.

None of the other variables we examined were significantly associated with gestation length. Previous studies show that female red squirrel body mass and body composition have limited effects on reproduction (Humphries and Boutin 1996). Energy-intensive factors, such as larger litters or male-biased compositions, may not impose the same selective pressures on gestation length in red squirrels as they do in other species (Huber et al. 2001; Mysterud et al. 2009). Despite experimental manipulation, females that experienced food supplementation (Dantzer et al. 2022) or glucocorticoid manipulations (Westrick et al. 2021) did not exhibit changes in gestation length, further supporting the idea that gestation length is relatively stable in this species.

Regarding maternal age, yearlings and older females face different reproductive energy allocations (Descamps et al. 2007, 2008). Yearling females must balance growth and reproduction, as they are sexually mature but not yet fully grown (Descamps et al. 2007). Approximately two thirds of yearling females reproduce (McAdam et al. 2007), and those that do typically have higher-quality territories than their peers as a result of an earlier birth date (Descamps et al. 2006). In contrast, older females experiencing senescence allocate more energy toward reproductive success (Descamps et al. 2007). The majority of females in our study were between 2 and 6 years old, limiting the sample sizes of yearlings and oldest females, potentially masking any age-related effects on gestation length. These life history trade-offs across age classes may partly explain the observed stability in gestation length across the population.

Our findings underscore the stability of gestation length as a life history trait, even in the face of population-wide variations in resource abundance that influence other reproductive traits in red squirrels. Neither individual-level factors nor annual resource fluctuations significantly affected gestation length in our study. Understanding how life history traits, even those with low variability, respond to changing biotic and environmental conditions is crucial for predicting the dynamic relationship between populations and their environments (Hantak et al. 2021).

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Author contributions with total Dragon Kill Points (DKP; Martinig et al. 2025) from Table S2 alongside CRediT contributions: NJB (35 DKP), RMRB (28 DKP), AGM (10 DKP), BD (8 DKP), SB (7 DKP), JEL (5 DKP), and ARM (47 DKP).

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Data availability

Our data and code are available through a dedicated GitHub repository (https://github.com/martinig/gestation.git).

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Competing interests

We have no competing interests to declare.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjz-2025-0075.

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