Canadian Science Publishing

ARTICLE

Survival estimates of free-living arctic ground squirrels (*Urocitellus parryii*): effects of sex and biologging

Sara M. Wilbur, Cody E. Deane, Greg A. Breed, C. Loren Buck, Cory T. Williams, and Brian M. Barnes

Abstract: Hibernation is associated with long lifespan: on average, hibernating mammals live 15% longer than nonhibernators of equivalent mass. We investigated how survival varies with sex, season, and the deployment of biologgers in arctic ground squirrels (*Urocitellus parryii* (Richardson, 1825)), a widely distributed northern hibernator. The duration of hibernation in arctic ground squirrels differs markedly by sex: females hibernate 30% longer each year than males, a behavioural trait that could positively affect female survival. Additionally, males engage in aggressive territorial and food cache defense in spring and fall, which may decrease survival in this sex. From 13 years of mark–recapture data, we estimated apparent survival of arctic ground squirrels in Arctic Alaska (USA) using Cormack–Jolly–Seber models in program MARK. We found that females had higher annual survival ($\hat{\varphi}_{\mathrm{F}}^{\mathrm{annual}} = 0.753$ (95% confidence interval (CI): 0.469, 0.913)) than males ($\hat{\varphi}_{\mathrm{M}}^{\mathrm{annual}} = 0.546$ (95% CI: 0.416, 0.670)), with a maximum observed lifespan (10 years) that exceeded that of males (6 years). We also show that biologger use and implantation did not significantly impact survival. Quantifying basic arctic ground squirrel demographics from this well-studied population illustrates how sex-specific hibernation parameters may influence lifespan differences in male and female arctic ground squirrels and provides support for the safety of biologging devices.

Key words: survival, lifespan, hibernation, biologging, arctic ground squirrel, Cormack–Jolly–Seber modeling, demographics, *Urocitellus parryii*.

Résumé : L'hibernation est associée à la durée de vie : en moyenne, les mammifères qui hibernent vivent 15 % plus longtemps que les mammifères de masse semblable qui n'hibernent pas. Nous examinons les variations de la survie en fonction du sexe, de la saison et du déploiement de capteurs de paramètres biologiques chez le spermophile arctique (*Urocitellus parryii* (Richardson, 1825)), un mammifère nordique hibernant caractérisé par une vaste répartition géographique. La durée de l'hibernation des spermophiles arctiques diffère considérablement selon le sexe : les femelles hibernant 30 % plus longtemps chaque année que les mâles, un caractère comportemental qui pourrait avoir une incidence positive sur la survie des femelles. En outre, les mâles s'adonnent à la défense agressive de leur territoire et de leurs caches de nourriture au printemps et à l'automne, ce qui peut réduire la survie chez ce sexe. À la lumière de 13 années de données de marquage–recapture, nous estimons le taux de survie apparent de spermophiles arctiques en Alaska arctique (États-Unis) en utilisant des modèles de Cormack–Jolly–Seber dans le programme MARK. Nous constatons que les femelles ont un plus haut taux de survie annuel ($\hat{\varphi}_{\mathrm{F}}^{\mathrm{annuel}} = 0{,}753$ (l'intervalle de confiance (IC) de 95 % : 0,469, 0,913)) que les mâles ($\hat{\varphi}_{\mathrm{M}}^{\mathrm{annuel}} = 0{,}546$ (IC de 95 % : 0,416, 0,670)) et une durée de vie maximum observée (10 ans) plus grande que celle des mâles (6 ans). Nous démontrons également que l'utilisation et l'implantation de capteurs de paramètres biologiques n'a pas d'impact significatif sur la survie. La quantification de paramètres démographiques de base des spermophiles arctiques à la lumière de cette population bien étudiée illustre l'influence que peuvent avoir les variations selon le sexe de paramètres associés à l'hibernation sur les différences de durée de vie des spermophiles arctiques mâles et étaie l'argument voulant que les appareils d'enregistrement de paramètres biologiques soient sécuritaires. [Traduit par la Rédaction]

Mots-clés : survie, durée de vie, hibernation, enregistrement de paramètres biologiques, spermophile arctique, modélisation Cormack–Jolly–Seber, démographie, *Urocitellus parryii*.

Introduction

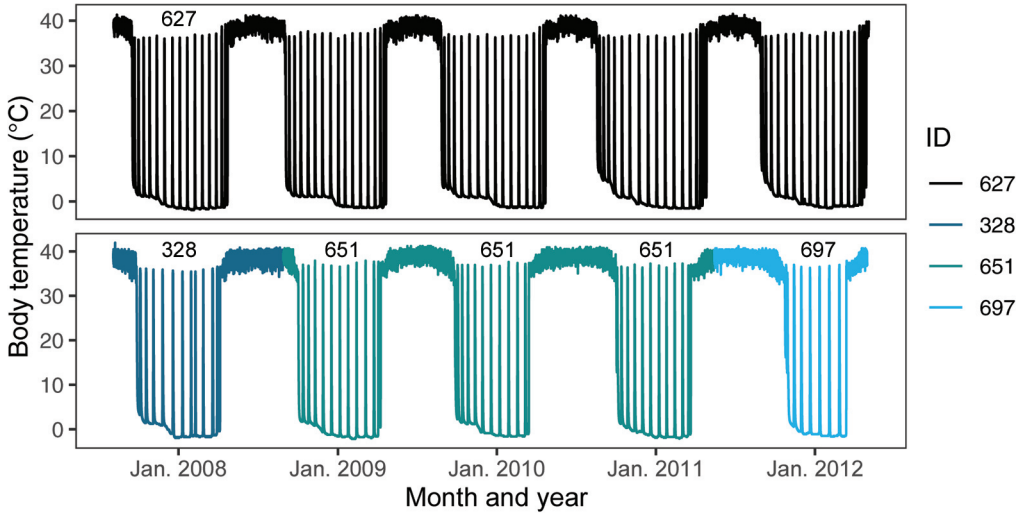
Hibernation is a strategy used by diverse species of mammals to survive prolonged resource scarcity (Geiser 1998; Staples 2016) and is associated with long lifespan: Turbill et al. (2011) determined that, on average, individual hibernating mammals exhibit 15% higher annual survival and live longer than nonhibernators of equivalent mass. The long intervals of sequestered inactivity characteristic of hibernation usually take place in a burrow or cave, which protects the animal from direct exposure and predation and in turn supports high overwinter survival (Turbill et al. 2011; Bieber et al. 2012). Furthermore, the ability of a hibernator to substantially reduce its whole-body and tissue-specific metabolic rates for extended periods — thereby decreasing its overall pace of life —

Received 11 August 2021. Accepted 29 November 2021.

S.M. Wilbur,[*,†] **C.E. Deane,**[*] **G.A. Breed, C.T. Williams,**[‡] **and B.M. Barnes.** University of Alaska Fairbanks, Fairbanks, AK 99775, USA.
C.L. Buck. Northern Arizona University, Flagstaff, AZ 86011, USA.

Corresponding author: Sara M. Wilbur (email: swilbur@tgen.org).
[*]These authors contributed equally to the manuscript.
[†]Present address: Translational Genomics Research Institute, Flagstaff, AZ 86005, USA.
[‡]Present address: Colorado State University, Fort Collins, CO 80523, USA.
© 2022 The Author(s). Permission for reuse (free in most cases) can be obtained from copyright.com.

Fig. 1. Body temperature patterns for one free-living arctic ground squirrel (*Urocitellus parryii*) female (top panel) and three free-living arctic ground squirrel males (shown sequentially; bottom panel) across 5 years (August 2007–April 2012). Colour version online.



may also contribute to increased lifespan (Lyman et al. 1981; Wu and Storey 2016). Although we have a basic understanding of the relationships among hibernation, survival, and lifespan, sex-specific differences in these demographic parameters have not been studied extensively, especially within natural populations of animals. Most vertebrates — including humans — exhibit sexual dimorphism in survival and longevity, which may be driven by differences in how the sexes optimize fundamental trade-offs between reproduction and survival (Clutton-Brock and Parker 1992; Bonduriansky et al. 2008; Maklakov and Lummaa 2013). Among polygynous vertebrates, for example, males have higher annual rates of mortality than females, in part due to intraspecies aggression during reproductive competition (Clutton-Brock and Isvaran 2007). In hibernating species, sex-specific differences in hibernation phenology (length of hibernation and (or) when immergence and emergence occur; Sheriff et al. 2013) and aboveground behaviour may also drive differences in survival and maximum lifespan between males and females.

Arctic ground squirrels (*Urocitellus parryii* (Richardson, 1825)) are the northernmost and largest ground squirrel species and an important prey animal for a variety of northern carnivores and raptors (Wheeler and Hik 2013; Robinson et al. 2019). The sexes differ in their hibernation timing; in northern Alaska, adult females enter hibernation in August or early September and begin to emerge in late April, while adult males hibernate for a shorter period, entering their hibernacula by early October and emerging by early to mid-April (Carl 1971; Sheriff et al. 2011). These sex-specific hibernation patterns are endogenously programmed and generally consistent across years (Fig. 1), although may be subject to phenotypic plasticity driven by changing environmental conditions (Williams et al. 2014*a*, 2014*b*). The sexes also differ in aboveground activity patterns, with males (but not females) dispersing prior to or after their first hibernation season (Byrom and Krebs 1999; Buck and Barnes 1999) and engaging in aggressive male–male conflicts in the spring (to defend access to mates; Lacey and Wieczorek 2001) and fall (to defend food caches; Buck and Barnes 2003; Richter et al. 2017). Finally, adult breeding male arctic ground squirrels (but not adult nonbreeding or juvenile males) exhibit an adaptive stress response that may favor reproduction over survival (Boonstra et al. 2001). It is assumed that female arctic ground squirrels do not undergo such an extreme trade-off; in other species of ground squirrels, females experience lower levels of mortality after breeding than do males (e.g., Sherman and Morton 1984; Michener and McLean 1996). Furthermore, female ground squirrel survival has been shown to not differ between animals that did and did not wean litters (Michener and Locklear 1990).

Arctic ground squirrels have been captured in Arctic Alaska near the Atigun River since the early 1990s to study hibernator physiology, life history, and phenology (e.g., Buck and Barnes 1999; Sheriff et al. 2011; Wilsterman et al. 2015; Williams et al. 2017; Chmura et al. 2020). These studies have often used biologging devices, including collar-mounted loggers that record light and temperature, collar-mounted accelerometers, and temperature loggers that are implanted into the abdominal cavity via surgery. While this prior work has revealed sex differences in hibernation phenology and circadian and diurnal patterns, the consequences of the resultant sexual dimorphism on demographic parameters — such as survival — are lacking. Here, we estimate sex differences in apparent seasonal survival of adult arctic ground squirrels with a retrospective analysis of the capture–recapture data that we collected during previous studies. Importantly, attaching or implanting biologging devices may impact the behaviour, susceptibility to predation, or survival of an animal (e.g., Van Vuren 1989; Berteaux et al. 1996; Murray and Fuller 2000). For these reasons, we also examined the effect of biologger deployment on survival. We predicted that (*i*) arctic ground squirrels would have comparable maximum lifespans — after controlling for body mass — to other hibernating species; (*ii*) shorter hibernation seasons and risky behaviour exhibited by male arctic ground squirrels would lead to reduced lifespan and survival relative to females; (*iii*) as arctic ground squirrels are largely sequestered from predators, apparent seasonal survival would be higher for both sexes during the winter; and (*iv*) as biologging devices weigh <3% of arctic ground squirrel body mass (Sheriff et al. 2011), biologger deployment would not significantly impact survival.

Materials and methods

Study area

Arctic ground squirrels are semi-fossorial rodents with a Holarctic distribution that includes montane and Arctic Alaska (McLean 2018). All arctic ground squirrels in this study were located in the northern foothills of the Brooks Range adjacent to the Dalton Highway near the Atigun River (hereinafter Atigun; elevation 812 m) in Alaska, USA (68°27′N, 149°21′W). The study site is approximately 27 ha and comprises sandy substrate that slopes slightly downward toward the Atigun River. The region is

characterized by continuous permafrost overlain with a 1–2 m active layer of soil that thaws annually. For additional site characteristics see Sheriff et al. (2011).

Data collection

We captured arctic ground squirrels with Tomahawk Live Traps (14 cm × 14 cm × 40 cm; Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) baited with carrot and fitted with covers to protect from rain and sun. We set and checked traps between 0900 and 2200, weather permitting (arctic ground squirrels are sensitive to unfavorable environmental conditions and stay underground in inclement weather; Long et al. 2005; Williams et al. 2016). In general, trapping efforts were often focused on marking–recapturing biologger-equipped squirrels for various projects; however, all newly encountered adults were marked and recaptures of previously marked individuals were recorded, regardless of their biologger status. As the habitat immediately surrounding the study area has few burrows, we trapped the entire colony at this location. In an attempt to select animals that were less likely to disperse, we generally only equipped animals with biologgers that were captured near the centre of the colony, and we targeted our trapping efforts on this core area in an attempt to recapture animals equipped with implanted loggers and (or) collars. Please refer to the "Cormack–Jolly–Seber analyses" subsection for an explanation of how we accounted for different forms of heterogeneity in survival and detection probability in our capture–recapture data (Cormack 1964; Jolly 1965; Seber 1965).

Upon initial capture, we distinguished adult animals — which we define as arctic ground squirrels that had overwintered at least once — from young-of-the-year animals by their relatively large mass and molted pelage. At first capture, we gave animals an ear tag (Monel No. 1005-1 tag; National Band and Tag Co., Newport, Kentucky, USA). Beginning in 2014, most animals (82%–100%, depending on year) also received a passive integrated transponder (PIT) tag (Avid Identification Systems, Inc., Norco, California, USA), implanted subdermally between the scapulae. Prior to 2014, most animals were PIT-tagged only when first equipped with a biologger affixed to a collar or surgically implanted in the abdomen. As we documented significant ear-tag loss throughout our study, we included only PIT-tagged animals and only those that were initially captured or recaptured as adults.

For this study, we used capture–recapture data collected from individuals PIT-tagged between 2006 and 2018. Over this time, we deployed two types of biologging devices on arctic ground squirrels: light–temperature loggers and accelerometers were deployed on collars and temperature loggers were surgically implanted into the peritoneal cavity (Long et al. 2007). We used light–temperature loggers to determine when arctic ground squirrels emerged from their burrows or were below ground (based on exposure to light), as well as when animals were torpid, aroused, or active (based on body temperature; Williams et al. 2016). Three types of light–temperature loggers were deployed on collars: BAS model MK7290 light loggers (1 g; Biotrack Ltd., Dorset, UK), Intigeo-C56 light loggers (1 g; Migrate Technology Ltd., Cambridge, UK), and GeoLT light loggers (8 g; Earth and Ocean Technologies, Kiel, Germany). Accelerometers (axy-3 and axy-4 loggers; less than 3 g; TechnoSmArt Europe Srl, Colleverde, Italy) affixed to collars were used for monitoring daily patterns of movement. Implanted temperature loggers were used to measure patterns of core body temperature during both active and hibernation seasons. We implanted–explanted two types of body temperature loggers in the abdominal cavities of squirrels between 2006 and 2018: modified TidbiTs (StowAway model TBICU32-05þ44; 12–14 g; Onset Computer Corporation, Bourne, Massachusetts, USA) and iButtons (model DS1922L; ~5 g; Maxim Integrated Products, Sunnydale, California, USA); for surgical details see Sheriff et al. (2011).

Cormack–Jolly–Seber analyses

We implemented our suite of Cormack–Jolly–Seber candidate models in program MARK version 8.2 (White and Burnham 1999) via R (R Core Team 2020) with the RMark package (Laake 2013). As we captured arctic ground squirrels following their spring emergence from their hibernacula (median capture date of 7 May) and in early August before females begin hibernation (median capture date of 4 August), we estimated "seasonal" apparent survival to better meet the assumption of demographic closure during capture occasions; therefore, apparent summer survival ($\hat{\varphi}_{\text{summer}}$) during year t is the probability of surviving during the period May_t to August_t, whereas apparent winter survival is the probability of surviving from August_t to May_{t+1} ($\hat{\varphi}_{\text{winter}}$). Hereinafter, for simplicity, we use the term "survival" in place of "apparent survival" and "detection" in place of "detection probability".

We accounted for expected sources of variation in survival and detection among individual arctic ground squirrels with several time-varying, individual covariates. First, we accounted for increased trapping effort for individuals with collars or implanted temperature loggers by constructing a time-varying individual covariate for each occasion when an arctic ground squirrel was expected to have either or both types of biologging devices ("device"). The device covariate was only considered to be a covariate for detection. We also considered two survival covariates (one for surgery and one for collars) that allowed us to evaluate potential impacts of biologging on survival. The surgery covariate was a time-varying, individual covariate corresponding to occasions during which a squirrel was operated on at least once to implant or explant a body temperature logger ("surgery"). The collar covariate was a time-varying, individual covariate for squirrels that wore a collar between trapping occasions ("collar"). For each time-varying covariate, a "1" indicated presence or instance of a device, surgery, or collar, whereas a "0" indicated absence or instance of a collar or surgery.

Preliminary analysis provided results consistent with field observations that some arctic ground squirrels displayed strong trap-response (i.e., "trap-happy") behaviour. We hypothesized that this trap-response behaviour could explain variation in survival or detection, which led us to construct models that included recapture information as covariates. We estimated survival relative to the number of times a squirrel was trapped throughout a survival interval (e.g., $\varphi_{t-(t+1)} \sim \text{trap}_t$), and estimated detection relative to the number of times an individual was captured during the previous occasion ($p_{t+1} \sim \text{trap}_t$). We also hypothesized that survival may decrease with age, so we considered models with age covariates that increased by one unit during each capture occasion (Table 1). Although we did not expect detection to vary with age, we also included models that allowed for this possibility (Table 1).

Given that male and female arctic ground squirrels differ in their phenology and patterns of energy expenditure across the annual cycle (Sheriff et al. 2011; Chmura et al. 2020), we specified a sex × season interaction in models for survival and detection ($\varphi_{\text{sex}\times\text{season}}\ p_{\text{sex}\times\text{season}}$). Data limitations rendered some estimates from time-varying models unidentifiable (e.g., $\varphi_{\text{sex}\times\text{season}+\text{occasion}}\ p_{\text{sex}\times\text{season}+\text{occasion}}$ or $\varphi_{\text{sex}\times\text{season}\times\text{occasion}}\ p_{\text{sex}\times\text{season}\times\text{occasion}}$). To circumvent our inability to implement a model with full-time variation in survival and detection, we accounted for annual variation in survival by grouping encounter occasions into the active season ($\varphi_{\text{sex}\times\text{season}+\text{active}}\ p_{\text{sex}\times\text{season}+\text{active}}$) or the hibernation season ($\varphi_{\text{sex}\times\text{season}+\text{hibernation}}\ p_{\text{sex}\times\text{season}+\text{hibernation}}$). For the time factor "active", we assigned the same factor level to May and August encounter occasions within the same calendar year (active_t groups the May_{year} capture occasion with $\text{August}_{\text{year}}$ occasion of the same year); these parameters are associated with changes in survival and detection that primarily occur over the summer. In contrast, the treatment of the factor "hibernation" was associated with the overwintering season; we assigned the same factor level to occasions occurring in August of a given calendar year and May of the subsequent calendar year (hibernation_t grouped $\text{August}_{\text{year}}$ with $\text{May}_{\text{year+1}}$). We then included active_t and hibernation_t in survival models without a priori

Table 1. Model structures for 32 models that estimated apparent survival (φ) and four models that estimated detection probability (p) in free-living arctic ground squirrels (*Urocitellus parryii*).

Model structures for φ and p	Model structures for φ and p continued
$\varphi_{\text{sex}\times\text{season}+\text{hibernation}+\text{collar}+\text{surgery}}$	$\varphi_{\text{sex}\times\text{season}+\text{trap}+\text{hibernation}+\text{surgery}}$
$\varphi_{\text{sex}\times\text{season}+\text{active}+\text{collar}+\text{surgery}}$	$\varphi_{\text{sex}\times\text{season}+\text{trap}+\text{active}+\text{surgery}}$
$\varphi_{\text{sex}\times\text{season}+\text{hibernation}+\text{surgery}}$	$\varphi_{\text{sex}\times\text{season}+\text{trap}+\text{hibernation}+\text{collar}}$
$\varphi_{\text{sex}\times\text{season}+\text{active}+\text{surgery}}$	$\varphi_{\text{sex}\times\text{season}+\text{trap}+\text{active}+\text{collar}}$
$\varphi_{\text{sex}\times\text{season}+\text{hibernation}+\text{collar}}$	$\varphi_{\text{sex}\times\text{season}+\text{trap}+\text{hibernation}}$
$\varphi_{\text{sex}\times\text{season}+\text{active}+\text{collar}}$	$\varphi_{\text{sex}\times\text{season}+\text{trap}+\text{active}}$
$\varphi_{\text{sex}\times\text{season}+\text{hibernation}}$	$\varphi_{\text{sex}\times\text{season}+\text{trap}+\text{age}+\text{hibernation}+\text{collar}+\text{surgery}}$
$\varphi_{\text{sex}\times\text{season}+\text{active}}$	$\varphi_{\text{sex}\times\text{season}+\text{trap}+\text{age}+\text{active}+\text{collar}+\text{surgery}}$
$\varphi_{\text{sex}\times\text{season}+\text{age}+\text{hibernation}+\text{collar}+\text{surgery}}$	$\varphi_{\text{sex}\times\text{season}+\text{trap}+\text{age}+\text{hibernation}+\text{surgery}}$
$\varphi_{\text{sex}\times\text{season}+\text{age}+\text{active}+\text{collar}+\text{surgery}}$	$\varphi_{\text{sex}\times\text{season}+\text{trap}+\text{age}+\text{active}+\text{surgery}}$
$\varphi_{\text{sex}\times\text{season}+\text{age}+\text{hibernation}+\text{surgery}}$	$\varphi_{\text{sex}\times\text{season}+\text{trap}+\text{age}+\text{hibernation}+\text{collar}}$
$\varphi_{\text{sex}\times\text{season}+\text{age}+\text{active}+\text{surgery}}$	$\varphi_{\text{sex}\times\text{season}+\text{trap}+\text{age}+\text{active}+\text{collar}}$
$\varphi_{\text{sex}\times\text{season}+\text{age}+\text{hibernation}+\text{collar}}$	$\varphi_{\text{sex}\times\text{season}+\text{trap}+\text{age}+\text{hibernation}}$
$\varphi_{\text{sex}\times\text{season}+\text{age}+\text{active}+\text{collar}}$	$\varphi_{\text{sex}\times\text{season}+\text{trap}+\text{age}+\text{active}}$
$\varphi_{\text{sex}\times\text{season}+\text{age}+\text{hibernation}}$	$p_{\text{sex}\times\text{season}+\text{device}+\text{trap}+\text{hibernation}}$
$\varphi_{\text{sex}\times\text{season}+\text{age}+\text{active}}$	$p_{\text{sex}\times\text{season}+\text{device}+\text{age}+\text{hibernation}}$
$\varphi_{\text{sex}\times\text{season}+\text{trap}+\text{hibernation}+\text{collar}+\text{surgery}}$	$p_{\text{sex}\times\text{season}+\text{device}+\text{trap}+\text{age}+\text{hibernation}}$
$\varphi_{\text{sex}\times\text{season}+\text{trap}+\text{active}+\text{collar}+\text{surgery}}$	$p_{\text{sex}\times\text{season}+\text{device}+\text{season}\times\text{trap}+\text{hibernation}}$

Note: All models for φ and p include separate intercepts for both sex classes (female and male) and both seasons (spring and autumn). Each model allowed for annual variation in both $\hat{\varphi}$ and $\hat{p}$ by grouping seasonal encounters by summer conditions (active; $\hat{\varphi}_{\text{spring}\,y}$ and $\hat{\varphi}_{\text{autumn}\,y}$) or by winter conditions (hibernation; $\hat{\varphi}_{\text{autumn}\,y}$ and $\hat{\varphi}_{\text{spring}\,y+1}$) in year y. For $\hat{\varphi}$, we also included parameters corresponding to wearing a collar during an encounter occasion (collar) or being operated on to deploy or retrieve a body temperature logger (surgery). For $\hat{p}$, we included a parameter that accounted for any squirrel wearing a device that we wanted to retrieve (device). For both $\hat{\varphi}$ and $\hat{p}$, we included parameters that accounted for the number of times a squirrel was captured at occasion t (trap). When trap was included in apparent survival models, the relationship was estimated between trap_t and $\hat{\varphi}_{t-(t+1)}$. When trap was included in detection models, the relationship was estimated between trap_t and $\hat{p}_{t+1}$.

expectation of which was most appropriate for these data; both covariates were included to best account for annual variation in survival while recognizing that it was possible that annual variation in survival could primarily be driven by conditions experienced during summer (May–August), winter (August–May), or both. We constructed a similar time factor to account for annual variation in detection, but only included models with the time factor hibernation_t because physiological research at our study site has focused on deploying devices after the breeding season, then recapturing animals after emergence in spring (Sheriff et al. 2011). We did not include models without time factors "hibernation" or "active" because trapping efforts and deployment of devices were inconsistent across years. Due to these variable efforts, we expected that variation in survival and detection were confounded with annual variation in environmental conditions (for details on how encounter occasions were grouped by season see Supplementary material).[1]

In total, we considered 32 candidate models for survival and 4 models for detection (128 model combinations; Table 1). We evaluated only a few covariates that could explain variation in survival; the abundance of models for survival was primarily a consequence of systematically evaluating covariates for surgery and collar along with the covariates for age and trap-response behaviour. In this suite of candidate models, we assessed relative support for our models using the information-theoretic approach (Burnham and Anderson 2002).

Goodness-of-fit testing for our models was complicated by our reliance on individual covariates; the median $\hat{C}$ procedure for assessing goodness-of-fit in program MARK does not allow parameters that estimate relationships between individual covariates and survival or detection. The median $\hat{C}$ value from our most parameterized model ($\varphi_{\text{sex}\times\text{season}+\text{hibernation}}\ p_{\text{sex}\times\text{season}+\text{hibernation}}$) was 4.665, which indicated that our model-selection results should be adjusted due to a lack of independence among the observed capture histories (Williams et al. 2002: p. 436). Therefore, we evaluated relative model support using Akaike's information criterion corrected for overdispersion (QAIC_c) values instead of Akaike's information criterion corrected for small sample size (AIC_c) values, which are model-selection values calculated using a formulation of AIC_c that effectively applies larger penalties to more complex models when compared with AIC_c (Burnham and Anderson 2002). Generally, AIC_c and QAIC_c values are interpreted similarly such that well-supported models are those falling within two QAIC_c units of the top model ($\Delta\text{QAIC}_c < 2$; Williams et al. 2002: pp. 433 and 434). When we adjusted AIC_c values to QAIC_c values, model-selection uncertainty increased; therefore, we display the model-selection results for the 17 most-supported models with relative model weights ≥0.02 (Table 2; $\Delta\text{QAIC}_c < 3.05$).

During preliminary analysis, we found that including models without annual time factors changed the results of our model selection such that individual covariates received greater weight when compared with the results that we present here; that is, covariates received more support from the data when not accounting for annual variation in survival and trapping effort. However, implementing models with seasonal survival periods with annual time factors complicated the calculation of standard errors of annual survival estimates (which are derived parameters); therefore, calculating the standard errors of female and male annual survival required implementation of the delta method (Williams et al. 2002: pp. 736 and

[1]Supplementary material and tables are available with the article at https://doi.org/10.1139/cjz-2021-0156.

Table 2. Model-selection results for the 17 most-supported Cormack–Jolly–Seber models that estimated apparent survival (φ) and detection probability (p) in free-living arctic ground squirrels (*Urocitellus parryii*).

Apparent survival	Detection probability	K	$\Delta QAIC_c$	w_i	$\sum w_i$
$\varphi_{sex\times season+age+hibernation}$	$p_{sex\times season+device+trap+hibernation}$	34	0.00	0.07	0.07
$\varphi_{sex\times season+age+hibernation}$	$p_{sex\times season+device+season\times trap+hibernation}$	35	0.09	0.07	0.14
$\varphi_{sex\times season+trap+age+hibernation}$	$p_{sex\times season+device+season\times trap+hibernation}$	36	1.13	0.04	0.18
$\varphi_{sex\times season+trap+age+hibernation}$	$p_{sex\times season+device+trap+hibernation}$	35	1.22	0.04	0.22
$\varphi_{sex\times season+age+active}$	$p_{sex\times season+device+trap+hibernation}$	34	1.79	0.03	0.25
$\varphi_{sex\times season+age+active}$	$p_{sex\times season+device+season\times trap+hibernation}$	35	1.82	0.03	0.28
$\varphi_{sex\times season+age+hibernation+collar}$	$p_{sex\times season+device+trap+hibernation}$	35	2.10	0.03	0.31
$\varphi_{sex\times season+age+hibernation+surgery}$	$p_{sex\times season+device+trap+hibernation}$	35	2.12	0.03	0.34
$\varphi_{sex\times season+age+hibernation}$	$p_{sex\times season+device+trap+age+hibernation}$	35	2.14	0.03	0.37
$\varphi_{sex\times season+age+hibernation+collar}$	$p_{sex\times season+device+season\times trap+hibernation}$	36	2.19	0.02	0.39
$\varphi_{sex\times season+age+hibernation}$	$p_{sex\times season+device+age+hibernation}$	34	2.19	0.02	0.41
$\varphi_{sex\times season+age+hibernation+surgery}$	$p_{sex\times season+device+season\times trap+hibernation}$	36	2.22	0.02	0.43
$\varphi_{sex\times season+hibernation}$	$p_{sex\times season+device+trap+hibernation}$	33	2.57	0.02	0.45
$\varphi_{sex\times season+hibernation}$	$p_{sex\times season+device+season\times trap+hibernation}$	34	2.70	0.02	0.47
$\varphi_{sex\times season+trap+age+active}$	$p_{sex\times season+device+season\times trap+hibernation}$	36	2.84	0.02	0.49
$\varphi_{sex\times season+trap+age+hibernation}$	$p_{sex\times season+device+age+hibernation}$	35	2.90	0.02	0.51
$\varphi_{sex\times season+trap+age+active}$	$p_{sex\times season+device+trap+hibernation}$	35	3.05	0.02	0.53

Note: We report the parameter count (K), the difference in Akaike's information criterion corrected for small sample size (AIC_c) and corrected for overdispersion ($QAIC_c$) between each model and the most-supported model ($\Delta QAIC_c$), the relative model weight (w_i), and the cumulative model weights ($\sum w_i$). We truncated the table to only include models with $w_i \geq 0.02$. The $QAIC_c$ value of the most-supported model was 426.23.

737), which is a method for approximating the variance for a function of random variables implemented in program MARK.

We circumvented this issue by fitting the two most-supported models without accounting for annual variation in survival: $\varphi_{sex\times season+age}\ p_{sex\times season+device+trap+hibernation}$ and $\varphi_{sex\times season+age}\ p_{sex\times season+device+season\times trap+hibernation}$. We then model-averaged estimates of seasonal and annual survival from these top two models. We found the point estimates of survival were equivalent to two decimal places when estimated by the top two models, regardless of whether we accounted for annual variation in apparent survival or not. Finally, we calculated the standard errors of annual survival estimates using the delta method (Williams et al. 2002) and calculated expected lifespan (E) using the equation (Krementz et al. 1989):

$$E = -\frac{1}{\ln(\varphi\text{annual})}$$

Ethics approval

The Institutional Animal Care and Use Committee at the University of Alaska Fairbanks approved all studies that are included in the article, and all studies followed the guidelines of the American Society of Mammalogists (Sikes et al. 2011). The Alaska Department of Fish and Game provided permits for all studies included in the article.

Results

Over the 13 years of our study, we recorded 1158 adult encounters of 157 adult female arctic ground squirrels and 1392 adult encounters of 177 adult male arctic ground squirrels. From these encounters, we obtained 362 unique recapture occasions of adult females (i.e., ≥1 recapture of one individual during a given encounter occasion) and 281 unique recapture occasions of males (for release and recapture details see Supplementary Table S1; for sample size information regarding collars and surgeries see Supplementary Table S2).[1]

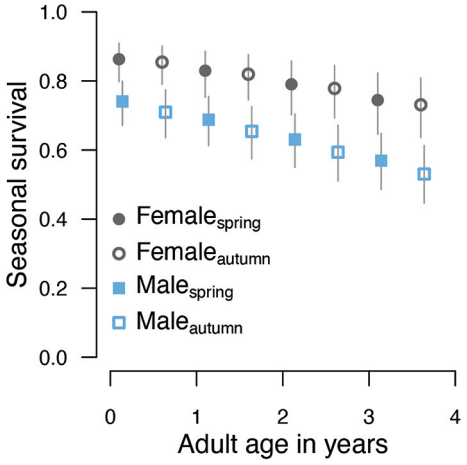
We report model-selection uncertainty between the candidate models; however, our two most-supported models ($\sum w_i = 0.14$; Table 2) revealed that seasonal survival decreased with age ($\hat{\beta}_{\varphi}^{age} = -0.152 \pm 0.033$, mean ± SE; Fig. 2) and that trap-response behaviour was positively related to subsequent detection (Figs. 3A and 3B). The two most-supported models differed in that the top model allowed detection to vary relative to the trap-response behaviour ($\hat{\beta}_{p}^{trap} = 0.203 \pm 0.067$; Table 2), while the second most-supported model allowed for the interaction season × trap when estimating detection ($\hat{\beta}_{p}^{trap,spring} = -0.009 \pm 0.073$, $\hat{\beta}_{p}^{trap,autumn} = 0.382 \pm 0.094$; Table 2). The second most-supported model estimated a positive relationship between the number of times a squirrel was captured in spring and detection during the subsequent autumn ($\hat{\beta}_{p}^{trap,autumn} = 0.382 \pm 0.094$); however, there was no relationship between the number of times a squirrel was captured in autumn and detection during the subsequent spring ($\hat{\beta}_{p}^{trap,spring} = -0.009 \pm 0.073$).

The third and fourth most-supported models differed from the first two models in that the number of times a squirrel was captured during an occasion was a covariate for seasonal survival in addition to detection ($\sum w_i = 0.08$; Table 2). These two models estimated that survival was positively related to the number of times a squirrel was captured at the beginning of a survival interval ($\hat{\beta}_{\varphi}^{trap} = 0.100 \pm 0.050$ and $\hat{\beta}_{\varphi}^{trap} = 0.083 \pm 0.042$, respectively). The estimated relationship between detection and trap-response behaviour was not weaker when trap-response behaviour was included as a covariate for survival; the third most-supported model estimated $\hat{\beta}_{p}^{trap,autumn} = 0.361 \pm 0.095$ and $\hat{\beta}_{p}^{trap,spring} = -0.025 \pm 0.072$, whereas the fourth most-supported model estimated $\hat{\beta}_{p}^{trap} = 0.182 \pm 0.068$. The fifth and sixth most-supported models were of the same structure as the two most-supported models, except that the time factor "active" replaced the time factor "hibernation" ($w_i = 0.03$; Table 2).

Models that allowed seasonal survival to vary relative to collar status ($\Delta QAIC_c = 2.11$) or surgery status ($\Delta QAIC_c = 2.13$) provided little evidence for decreased survival ($\hat{\beta}_{collar} = 0.117 \pm 0.231$, mean ± SE; $\hat{\beta}_{surgery} = 0.078 \pm 0.208$). We found that detection was higher for animals wearing biologging devices (collars, implanted temperature loggers, or both) since our two most-supported and second most-supported models estimated strong, positive relationships between our covariate "device" and "detection" ($\hat{\beta}_{device} = 0.701 \pm 0.251$ and $\hat{\beta}_{device} = 0.765 \pm 0.256$, respectively).

Of the covariates that we evaluated for their relationship to apparent survival, age was included in our 12 most-supported

Fig. 2. Apparent seasonal survival of free-living arctic ground squirrels (*Urocitellus parryii*) relative to observed age captured at Atigun Pass, Alaska, USA, 2006–2018. We use the term "observed age" because these results are primarily composed of individuals captured as unknown-age adults; therefore, age is not absolute (for example, age 1 corresponds to the first capture of an adult arctic ground squirrel during the spring capture occasion of a given year *t*). The spring age estimates represent seasonal survival from May$_t$ to August$_t$, whereas autumn age estimates represent seasonal survival from August$_t$ to May$_{t+1}$. Colour version online.



models (w_i = 0.44; Table 2). The two most-supported models indicated that survival decreased for squirrels as they aged since both models estimated $\hat{\beta}_{\varphi}^{\text{age}} = -0.152 \pm 0.033$ (Fig. 2). Trap-response behaviour was included as a covariate for seasonal survival in two models with $\Delta\text{QAIC}_c \geq 3.0$ ($\sum w_i = 0.08$; Table 2). The cumulative inference from our models with $w_i \geq 0.02$ is that the negative relationship between seasonal survival and age ($\sum w_i = 0.49$) was much stronger than the positive relationship between seasonal survival and trap-response behaviour ($\sum w_i = 0.14$; Table 2). Among the models for which $\Delta\text{QAIC}_c \geq 2.0$, there was more support for the time factor "hibernation" ($\sum w_i = 0.41$) than for the time factor "active" ($\sum w_i = 0.12$; Table 2).

We found that males had lower survival than females during both seasons, but that survival did not vary with season, as $\hat{\varphi}_{\text{F}}^{\text{winter}} = 0.870$ (95% confidence interval (CI): 0.807, 0.914), $\hat{\varphi}_{\text{F}}^{\text{summer}} = 0.866$ (95% CI: 0.795, 0.914), $\hat{\varphi}_{\text{M}}^{\text{winter}} = 0.736$ (95% CI: 0.661, 0.800), and $\hat{\varphi}_{\text{M}}^{\text{summer}} = 0.742$ (95% CI: 0.668, 0.804). The product of these seasonal survival estimates resulted in annual survival estimates of $\hat{\varphi}_{\text{F}}^{\text{annual}} = 0.753$ (95% CI: 0.469, 0.913) and $\hat{\varphi}_{\text{M}}^{\text{annual}} = 0.546$ (95% CI: 0.416, 0.670). These estimates of annual survival correspond to expected lifespans of 3.518 years (95% CI: 1.321, 10.960) for females and 1.651 years (95% CI: 1.140, 2.494) for males. The estimates of seasonal and annual survival that we report here, in addition to the associated estimates of expected lifespan, are for adult arctic ground squirrels 1 year after their initial capture and do not account for low survival of juveniles or senescing survival of arctic ground squirrels. Based on ear-tag data from a longer time frame (1990–2018), we documented a maximum lifespan of 10 years for one female and 6 years for one male; owing to high ear tag loss, we cannot estimate mean lifespan from this older dataset.

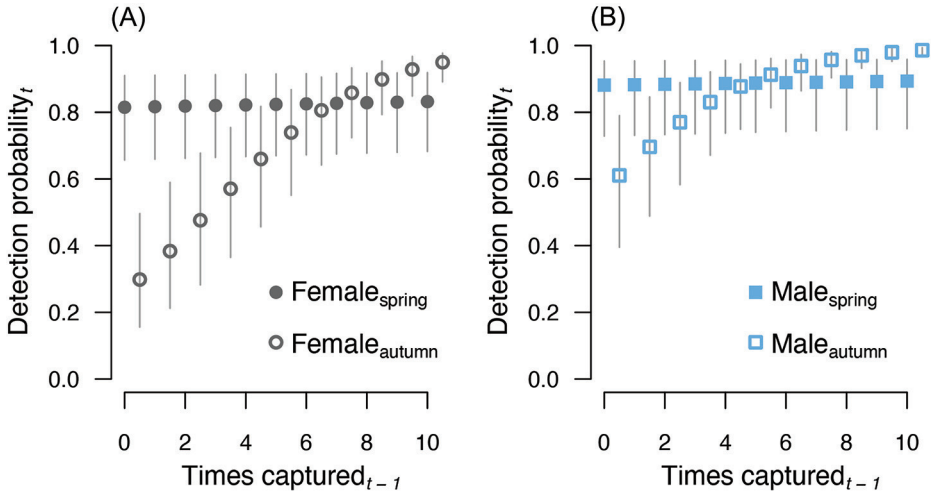
Discussion

The physiology, phenology, and behaviour of arctic ground squirrels has been studied extensively for decades, yet basic demographic information in natural populations, including seasonal or annual survival, has not yet been reported. Based on mark–recapture analyses of PIT-tagged squirrels, we found that females have higher survival probability than males and, accordingly, higher expected lifespans; this was consistent with an observed maximum female lifespan of 10 years from ear-tagging data. Higher survival probability in female arctic ground squirrels is consistent with sex-specific lifespan differences in other rodent species (Clutton-Brock and Isvaran 2007; Barrett and Richardson 2011); when compared with hibernators of similar mass (male arctic ground squirrels weigh 600–1000 g, with some reports of male masses above 1 kg, whereas females weigh about 10%–30% less, depending on season; McLean 2018; Zhang et al. 2020), the maximum lifespans for both sexes of arctic ground squirrel generally coincide with the lifespans of other similar-sized hibernators.

Longer lifespans in females compared with males is common in vertebrate species where the male competes with other males for reproductive opportunities with associated injuries and exposure to predation (Clutton-Brock and Isvaran 2007; Maklakov and Lummaa 2013; alternatively, differences in lifespan may be due to sex-specific genetic causes (Tower and Arbeitman 2009) or to selection for longer life in the caregiving sex (Young et al. 2013)). The propensity of females to outlive males is common across ground squirrel species, including Richardson's (*Urocitellus richardsonii* (Sabine, 1822); Michener 1989), Townsend's (*Urocitellus townsendii* (Bachman, 1839); Smith and Johnson 1985), and Uinta (*Urocitellus armatus* (Kennicott, 1863); Rieger 1996) ground squirrels. One behavioural aspect that differs between these other ground squirrel species and arctic ground squirrels is the dissimilarity in hibernation duration between male and female arctic ground squirrels (Fig. 1). Female arctic ground squirrels hibernate as much as 30% longer each year than males, immerging into their hibernacula in August and emerging by late April, whereas males enter hibernation as late as October and emerge in early April (Carl 1971; Sheriff et al. 2011), while ending the heterothermic portion of hibernation 3 weeks earlier (Williams et al. 2017; Fig. 1). In contrast, differences in hibernation duration between the sexes are much smaller in other hibernating ground squirrel species. For example, the onset and termination of hibernation occur at similar times of the year in both sexes of thirteen-lined ground squirrels (*Ictidomys tridecemlineatus* (Mitchill, 1821)), and females only marginally outlive males (McCarley 1966). In Townsend's ground squirrels, females emerge from hibernation 1 to 2 weeks later than males and also appear to only slightly outlive males (Smith and Johnson 1985; immergence times were not reported). Similar to our findings, Michener (1989) reported that, in a population of Richardson's ground squirrels, females outlived males by 2 years (6-year maximum lifespan for females; 4-year maximum lifespan for males). Overall, sex-specific differences in hibernation duration and in lifespan in arctic ground squirrels are more pronounced than in other ground squirrel species.

The sex-specific estimates of seasonal survival that we report here are consistent with previously published survival estimates reported for similar-sized hibernators (Turbill et al. 2011). However, an unexpected result from our analysis was the lack of a season-specific difference in survival in either males or females, as hibernation has been shown to confer protection from predation in several hibernating species (e.g., Broadbooks 1970; Schaub and Vaterlaus-Schlegel 2001; Bryant and Page 2005; Bieber et al. 2012). Our inability to detect differences in seasonal survival may be a consequence of trapping occasions imperfectly aligning with the timing of spring emergence and (or) fall immergence across years. For example, our estimates of winter survival encompass 4 August through 7 May of the following year; thus, any arctic ground squirrels that died before entering hibernation but after the last August trapping session, or after emergence but before May trapping efforts in spring, would bias low estimates of winter survival. Timing trapping to better coincide with emergence and immergence — in addition to adding a mid-summer

Fig. 3. Seasonal detection probability of free-living arctic ground squirrels (*Urocitellus parryii*) as a function of the number of times an individual was captured during the previous capture occasion (i.e., times captured) at Atigun Pass, Alaska, USA, 2006–2018. Results are for (A) females and (B) males. The *x* axis corresponds to the number of times a squirrel was captured at $t - 1$. That is, autumn estimates of detection probability in year *y* correspond to the number of times a squirrel was captured in spring$_y$. Detection probability in spring$_{y+1}$ was estimated relative to the number of times a squirrel was captured in autumn$_y$. Colour version online.



sampling occasion — would allow for better estimates of seasonal survival.

Estimated male summer survival may also be affected by the absence of trapping occasions during periods of spring and fall conspecific aggression. In early fall, male arctic ground squirrels remain active above ground to store and defend a food cache to be consumed the following spring prior to emergence (Buck and Barnes 2003). This defense of caches can become aggressive (Richter et al. 2017), a behaviour that repeats after emergence in mid-March when males compete for access to females prior to mating (Lacey and Wieczorek 2001); these interactions can result in injury or death (Batzli and Sobaski 1980). While such risky behaviours are common in hibernating sciurids, if male arctic ground squirrels are engaging in aggressive intrasexual interactions, favoring reproductive success over survival (as described in Boonstra et al. 2001), or dispersing during periods when females are still hibernating, it follows that males may experience higher mortality and, ultimately, lower summer survival. As these aggressive periods did not align well with our trapping occasions, winter survival as estimated is likely biased low and summer survival is biased high for males.

Our most-supported result is that survival rate declines with age, which we interpret to be indicative of arctic ground squirrels experiencing physiological senescence that is associated with increasing mortality risk. Conceivably, arctic ground squirrels could emigrate from our study population at increasing rates as they age, but we suspect this is an unlikely explanation for decreasing recapture rates of older squirrels and is inconsistent with mammalian dispersal behaviour, whereby dispersal is driven by young individuals (Byrom and Krebs 1999). Therefore, given abundant evidence for senescing survival of many mammal species (e.g., Kirkwood et al. 1991; Abrams 1993; McHugh and Gil 2018), this result is not surprising. A promising avenue for future research would be to estimate age-specific survival relative to physiological markers (such as telomere length; e.g., Boonekamp et al. 2014; Wilbur et al. 2019) so that ecologists can better understand the interactions between age-dependent survival, individual heterogeneity, and the mortality mechanisms that drive survival variation at the population level in arctic ground squirrels.

Although our results for survival and age are robust, we interpret one other result cautiously: greater support for the time factor "hibernation" relative to the time factor "active". Ecologically, we interpret support for hibernation to indicate that environmental conditions experienced between August$_{year}$ and May$_{year+1}$ to be more important to variation in survival of arctic ground squirrels than environmental conditions experienced between May$_{year}$ and August$_{year}$. Our confidence in support for "hibernation" relative to "active" is limited due to confounding between survival and emigration, the potential for emigration to be higher after the breeding season, and our inability to further explore variation in seasonal survival due to data limitations (i.e., our inability to fit a model in which survival and detection vary fully with time). Until monitoring efforts more consistently tag larger cohorts of arctic ground squirrels such that robust-design capture–recapture models can be used to estimate survival while accounting for emigration (Kendall et al. 1997), our knowledge about the seasonal and annual environmental conditions that drive variation in arctic ground squirrel survival will remain limited.

As the mark–recapture dataset used in this study was collected opportunistically, we used the Cormack–Jolly–Seber model structure to address weaknesses in the study design for modeling survival probability, although this ultimately limited our ability to make stronger conclusions regarding arctic ground squirrel survival. Most importantly, emigration and mortality could not be distinguished; therefore, our estimates of survival may be biased low. We expected that if emigration from our study site was substantial, there would have been more support for "trap" as a covariate for survival instead of as a covariate for detection. We interpret the positive relationship between "trap" and detection that varied with season as resulting from a behavioural mechanism such as socially dominant arctic ground squirrels being more willing to access the traps (for examples of socially dominant trap behaviour in other rodent species see Pawlina and Proulx 1999). However, we cannot rule out the possibility that a form of emigration leads to the seasonal interaction between detection and trap (Figs. 3A and 3B). It is possible the relationships displayed in Figs. 3A and 3B could result from squirrels with low trap affinity emigrating from the study site before the autumn trapping occasion (or being more likely to hibernate during the autumn trapping occasion), then immigrating back onto the study site before the spring trapping occasion, rendering them equally detectable across trapping occasions.

In addition to estimating annual survival estimates, we also analyzed how biologger deployment impacted arctic ground squirrel survival. A detailed review by Murray and Fuller (2000) investigated the effects of marking and biologger deployment on vertebrate biology and found that use of devices can have a wide range of effects on that animal's behaviour and (or) survival. Using radio transmitters (collar-deployed) as an example, studies of the effects of radio-transmitter deployment on meadow voles (*Microtus pennsylvanicus* (Ord, 1815)) showed varying results: one study reported no effect of deployment on behaviour (Berteaux et al. 1996), whereas others showed negative effects on activity (Hamley and Fall 1975), mass and survival (Webster and Brooks 1980), and social relationships (Berteaux et al. 1994). In larger mammals, the effects of collar-deployment also vary and appear to be driven by collar mass. For example, in domestic cats (*Felis catus* Linnaeus, 1758), collars below 2% of the animal's body mass had no effect on ranging distance, whereas larger collars (3% of body mass) reduced home-range size (Coughlin and van Heezik 2015). In plains zebras (*Equus burchelli antiquorum* (C.H. Smith, 1841)), slightly heavier GPS collars (0.6% vs. 0.4% of body mass) reduced travel rate by ~50% and interfered with grazing behaviour; both types of collars were within acceptable mass limits (Brooks et al. 2008). For arctic ground squirrels in our population, collars (devices that include an accelerometer, a light–temperature logger, or both) had little impact on estimates of survival. This is likely due to the minimally invasive nature of the collars, which are light in mass (~5 g, or 1% of body mass of a 500 g arctic ground squirrel) and are deployed with the logger epoxied to a continuous section of tubing to prevent neck abrasion (Williams et al. 2014*b*).

In contrast to collar deployment, surgeries to implant or remove body temperature loggers are more invasive (for our procedure details see Long et al. 2007). We found little evidence that use of internal loggers and associated surgeries in free-living arctic ground squirrels depressed survival. In relating our findings to the literature, we found that studies that have investigated the effects of peritoneal implants on small-mammal survival are scarce and somewhat outdated (e.g., Smith 1980; Eagle et al. 1984; Van Vuren 1989; Dausmann 2005). Furthermore, these studies did not use robust mark–recapture methods to test for the effect of implantation surgery on survival. Nevertheless, these few studies did not find a negative effect of implantation on survival, and the most common cause of mortality that did occur was from infection following surgery.

Our work offers new insight into the demographics of a free-living hibernating mammal occupying an extreme, arctic environment and provides interesting results that merit further investigation. Future work could gain insight into the relative role of senescence, individual quality, and climate in the seasonal survival and population dynamics of these hibernating mammals. As arctic ground squirrels are important ecological engineers and prey in northern ecosystems, the need to better understand their demography is critical given rapid climate-driven ecological change currently underway in the Arctic (Post et al. 2009; Hobbie et al. 2017).

Competing interests statement

The authors declare that there are no competing interests. The content is solely the responsibility of the authors and does not necessarily reflect the official views of the National Institutes of Health or the National Science Foundation.

Contributors' statement

S.M.W. — conceptualization, formal analysis, investigation, writing (original draft, review, and editing), and visualization. C.E.D. — formal analysis, resources, data curation, writing (original draft, review, and editing), and visualization. G.A.B. — formal analysis and writing (review and editing). C.L.B. — conceptualization, methodology, validation, investigation, writing (review and editing), supervision, project administration, and funding acquisition. C.T.W. — conceptualization, methodology, validation, investigation, writing (review and editing), supervision, project administration, and funding acquisition. B.M.B. — conceptualization, methodology, validation, investigation, writing (review and editing), supervision, project administration, and funding acquisition.

Funding statement

Research reported in this article was supported by grants from the National Science Foundation (NSF) to B.M.B. (IOS-1558160) and C.T.W. (IOS-1558056). Additionally, S.M.W. received fellowship support through an Institutional Development Award (IDeA) from the National Institute of General Medical Sciences of the National Institutes of Health (NIH) under grant number P20GM103395.

Acknowledgements

We thank those students and technicians who assisted in collecting data between 1990 and 2018 for the Institute of Arctic Biology's long-term arctic ground squirrel dataset. We also thank Matthew Dillon for curating the online arctic ground squirrel database. We appreciate Christa Mulder's initial encouragement and analysis suggestions. Finally, we acknowledge The Toolik Field Station for providing housing and laboratory space during trapping and biologger deployment.

References

Abrams, P.A. 1993. Does increased mortality favor the evolution of more rapid senescence? Evolution, **47**(3): 877–887. doi:10.1111/j.1558-5646.1993.tb01241.x. PMID:28567901.

Barrett, E.L.B., and Richardson, D.S. 2011. Sex differences in telomeres and lifespan. Aging Cell, **10**(6): 913–921. doi:10.1111/j.1474-9726.2011.00741.x. PMID:21902801.

Batzli, G.O., and Sobaski, S.T. 1980. Distribution, abundance, and foraging patterns of ground squirrels near Atkasook, Alaska. Arctic Alpine Res. **12**(4): 501–510. doi:10.2307/1550497.

Berteaux, D., Duhamel, R., and Bergeron, J.-M. 1994. Can radio collars affect dominance relationships in *Microtus*? Can. J. Zool. **72**(4): 785–789. doi:10.1139/z94-106.

Berteaux, D., Masseboeuf, F., Bonzom, J.-M., Bergeron, J.-M., Thomas, D.W., and Lapierre, H. 1996. Effect of carrying a radiocollar on expenditure of energy by meadow voles. J. Mammal. **77**(2): 359–363. doi:10.2307/1382808.

Bieber, C., Juškaitis, R., Turbill, C., and Ruf, T. 2012. High survival during hibernation affects onset and timing of reproduction. Oecologia, **169**(1): 155–166. doi:10.1007/s00442-011-2194-7. PMID:22095523.

Bonduriansky, R., Maklakov, A., Zajitschek, F., and Brooks, R. 2008. Sexual selection, sexual conflict and the evolution of ageing and life span. Funct. Ecol. **22**(3): 443–453. doi:10.1111/j.1365-2435.2008.01417.x.

Boonekamp, J.J., Mulder, G.A., Salomons, H.M., Dijkstra, C., and Verhulst, S. 2014. Nestling telomere shortening, but not telomere length, reflects developmental stress and predicts survival in wild birds. Proc. R. Soc. B Biol. Sci. **281**(1785): 20133287. doi:10.1098/rspb.2013.3287. PMID:24789893.

Boonstra, R., McColl, C.J., and Karels, T.J. 2001. Reproduction at all costs: The adaptive stress response of male arctic ground squirrels. Ecology, **82**(2): 1930–1946. doi:10.1890/0012-9658(2001)082[1930:RAACTA]2.0.CO;2.

Broadbooks, H.E. 1970. Home ranges and territorial behavior of the yellow-pine chipmunk, *Eutamias amoenus*. J. Mammal. **51**(2): 310–326. doi:10.2307/1378481.

Brooks, C., Bonyongo, C., and Harris, S. 2008. Effects of global positioning system collar weight on zebra behavior and location error. J. Wildl. Manage. **72**(2): 527–534. doi:10.2193/2007-061.

Bryant, A.A., and Page, R.E. 2005. Timing and causes of mortality in the endangered Vancouver Island marmot (*Marmota vancouverensis*). Can. J. Zool. **83**(5): 674–682. doi:10.1139/z05-055.

Buck, C.L., and Barnes, B.M. 1999. Annual cycle of body composition and hibernation in free-living arctic ground squirrels. J. Mammal. **80**(2): 430–442. doi:10.2307/1383291.

Buck, C.L., and Barnes, B.M. 2003. Androgen in free-living arctic ground squirrels: seasonal changes and influence of staged male–male aggressive encounters. Horm. Behav. **43**(2): 318–326. doi:10.1016/S0018-506X(02)00050-8. PMID:12694642.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer, New York.

Byrom, A.E., and Krebs, C.J. 1999. Natal dispersal of juvenile arctic ground squirrels in the boreal forest. Can. J. Zool. **77**(7): 1048–1059. doi:10.1139/z99-072.

Carl, E.A. 1971. Population control in Arctic ground squirrels. Ecology, **52**: 395–413. doi:10.2307/1937623.

Chmura, H.E., Zhang, V.Y., Wilbur, S.M., Barnes, B.M., Buck, C.L., and Williams, C.T. 2020. Plasticity and repeatability of activity patterns in free-living Arctic ground squirrels. Anim. Behav. **169**: 81–91. doi:10.1016/j.anbehav.2020.09.007.

Clutton-Brock, T.H., and Isvaran, K. 2007. Sex differences in ageing in natural populations of vertebrates. Proc. R. Soc. B Biol. Sci. **274**(1629): 3097–3104. doi:10.1098/rspb.2007.1138. PMID:17939988.

Clutton-Brock, T.H., and Parker, G.A. 1992. Potential reproductive rates and the operation of sexual selection. Q. Rev. Biol. **67**(4): 437–456. doi:10.1086/417793.

Cormack, R.M. 1964. Estimates of survival from the sighting of marked animals. Biometrika, **51**(3–4): 429–438. doi:10.1093/biomet/51.3-4.429.

Coughlin, C.E., and van Heezik, Y. 2015. Weighed down by science: Do collar-mounted devices affect domestic cat behaviour and movement? Wildl. Res. **41**(7): 606–614. doi:10.1071/WR14160.

Dausmann, K.H. 2005. Measuring body temperature in the field — evaluation of external vs. implanted transmitters in a small mammal. J. Them. Biol. **30**(3): 195–202. doi:10.1016/j.jtherbio.2004.11.003.

Eagle, T.C., Choromanski-Norris, J., and Kuechle, V.B. 1984. Implanting radio transmitters in mink and Franklin's ground squirrels. Wildl. Soc. Bull. **12**: 180–184.

Geiser, F. 1998. Evolution of daily torpor and hibernation in birds and mammals: Importance of body size. Clin. Exp. Pharmacol. Physiol. **25**(9): 736–740. doi:10.1111/j.1440-1681.1998.tb02287.x. PMID:9750966.

Hamley, J.M., and Fall, J.B. 1975. Reduced activity in transmitter-carrying voles. Can. J. Zool. **53**(10): 1476–1478. doi:10.1139/z75-179.

Hobbie, J.E., Shaver, G.R., Rastetter, E.B., Cherry, J.E., Goetz, S.J., Guay, K.C., et al. 2017. Ecosystem responses to climate change at a Low Arctic and a High Arctic long-term research site. Ambio, **46**(1): 160–173. doi:10.1007/s13280-016-0870-x. PMID:28116685.

Jolly, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika, **52**(1–2): 225–248. doi:10.1093/biomet/52.1-2.225. PMID:14341276.

Kendall, W.L., Nichols, J.D., and Hines, J.E. 1997. Estimating temporary emigration using capture–recapture data with Pollock's robust design. Ecology, **78**: 563–578. doi:10.2307/2266030.

Kirkwood, T.B.L., Rose, M.R., Harvey, P.H., Partridge, L., and Southwood, S.R. 1991. Evolution of senescence: late survival sacrificed for reproduction. Philos. Trans. R. Soc. Lond. B. Biol. Sci. **332**(1262): 15–24. doi:10.1098/rstb.1991.0028. PMID:1677205.

Krementz, D.G., Sauer, J.R., and Nichols, J.D. 1989. Model-based estimates of annual survival rate are preferable to observed maximum lifespan statistics for use in comparative life-history studies. Oikos, **56**(2): 203–208. doi:10.2307/3565337.

Laake, J.L. 2013. RMark: an r interface for analysis of capture–recapture data with MARK. AFSC Processed Rep. 2013-01. Alaska Fisheries Science Center, NOAA National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115, USA. 25 pp.

Lacey, E.A., and Wieczorek, J.R. 2001. Territoriality and male reproductive success in arctic ground squirrels. Behav. Ecol. **12**(5): 626–632. doi:10.1093/beheco/12.5.626.

Long, R.A., Martin, T.J., and Barnes, B.M. 2005. Body temperature and activity patterns in free-living arctic ground squirrels. J. Mammal. **86**(2): 314–322. doi:10.1644/BRG-224.1.

Long, R.A., Hut, R.A., and Barnes, B.M. 2007. Simultaneous collection of body temperature and activity data in burrowing mammals: a new technique. J. Wildl. Manage. **71**(4): 1375–1379. doi:10.2193/2006-399.

Lyman, C.P., O'Brien, R.C., Greene, G.C., and Papafrangos, E.D. 1981. Hibernation and longevity in the Turkish hamster *Mesocricetus brandti*. Science, **212**(4495): 668–670. doi:10.1126/science.7221552.

Maklakov, A.A., and Lummaa, V. 2013. Evolution of sex differences in lifespan and aging: Causes and constraints. Bioessays, **35**(8): 717–724. doi:10.1002/bies.201300021. PMID:23733656.

McCarley, H. 1966. Annual cycle, population dynamics and adaptive behavior of *Citellus tridecemlineatus*. J. Mammal. **47**(2): 294–316. doi:10.2307/1378126.

McHugh, D., and Gil, J. 2018. Senescence and aging: Causes, consequences, and therapeutic avenues. J. Cell. Biol. **217**(1): 65–77. doi:10.1083/jcb.201708092. PMID:29114066.

McLean, B.S. 2018. *Urocitellus parryii* (Rodentia: Sciuridae). Mammal. Spec. **50**(964): 84–99. doi:10.1093/mspecies/sey011.

Michener, G.R. 1989. Sexual differences in interyear survival and life-span of Richardson's ground squirrels. Can. J. Zool. **67**(7): 1827–1831. doi:10.1139/z89-260.

Michener, G.R., and Locklear, L. 1990. Differential costs of reproductive effort for male and female Richardson's ground squirrels. Ecology, **71**: 855–868. doi:10.2307/1937357.

Michener, G.R., and McLean, I.G. 1996. Reproductive behaviour and operational sex ratio in Richardson's ground squirrels. Anim. Behav. **52**(4): 743–758. doi:10.1006/anbe.1996.0219.

Murray, D.L., and Fuller, M.R. 2000. A critical review of the effects of marking on the biology of vertebrates. *In* Research techniques in animal ecology. 2nd ed. *Edited by* M.C. Pearl, L. Boitani, and T.K. Fuller. Columbia University Press, New York. pp. 15–64.

Pawlina, I., and Proulx, G. 1999. Factors affecting trap efficiency: a review. *In* Mammal trapping. *Edited by* G. Proulx. Alpha Wildlife Publishers, Sherwood Park, Alta. pp. 95–115.

Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., et al. 2009. Ecological dynamics across the Arctic associated with recent climate change. Science, **325**(5946): 1355–1358. doi:10.1126/science.1173113. PMID:19745143.

R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org/.

Richter, M.M., Barnes, B.M., O'Reilly, K.M., Fenn, A.M., and Buck, C.L. 2017. The influence of androgens on hibernation phenology of free-living male arctic ground squirrels. Horm. Behav. **89**: 92–97. doi:10.1016/j.yhbeh.2016.12.007. PMID:27986541.

Rieger, J.F. 1996. Body size, litter size, timing of reproduction, and juvenile survival in the Unita ground squirrel, *Spermophilus armatus*. Oecologia, **107**(4): 463–468. doi:10.1007/BF00333936. PMID:28307388.

Robinson, B.W., Booms, T.L., Bechard, M.J., and Anderson, D.L. 2019. Dietary plasticity in a specialist predator, the Gyrfalcon (*Falco rusticolus*): New insights into diet during brood rearing. J. Raptor Res. **53**(2): 115–126. doi:10.3356/JRR-15-58.

Schaub, M., and Vaterlaus-Schlegel, C. 2001. Annual and seasonal variation of survival rates in the garden dormouse (*Eliomys quercinus*). J. Zool. **255**(1): 89–96. doi:10.1017/S0952836901001133.

Seber, G.A.F. 1965. A note on the multiple-recapture census. Biometrika, **52**(1–2): 249–260. doi:10.1093/biomet/52.1-2.249. PMID:14341277.

Sheriff, M.J., Kenagy, G.J., Richter, M., Lee, T., Tøien, Ø., Kohl, F., et al. 2011. Phenological variation in annual timing of hibernation and breeding in nearby populations of Arctic ground squirrels. Proc. R. Soc. B Biol. Sci. **278**(1716): 2369–2375. doi:10.1098/rspb.2010.2482. PMID:21177687.

Sheriff, M.J., Richter, M.M., Buck, C.L., and Barnes, B.M. 2013. Changing seasonality and phenological responses of free-living male arctic ground squirrels: the importance of sex. Philos. Trans. R. Soc. B Biol. Sci. **368**(1624): 20120480. doi:10.1098/rstb.2012.0480. PMID:23836786.

Sherman, P.W., and Morton, M.L. 1984. Demography of Belding's ground squirrels. Ecology, **65**(5): 1617–1628. doi:10.2307/1939140.

Sikes, R.S., and Gannon, W.L. the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. J. Mammal. **92**(1): 235–253. doi:10.1644/10-MAMM-F-355.1.

Smith, G.W., and Johnson, D.R. 1985. Demography of a Townsend ground squirrel population in southwestern Idaho. Ecology, **66**(1): 171–178. doi:10.2307/1941317.

Smith, H.R. 1980. Growth, reproduction and survival in *Peromyscus leucopus* carrying intraperitoneally implanted transmitters. *In* A Handbook on Biotelemetry and Radio Tracking. *Edited by* C.J. Amlaner and D.W. MacDonald. Pergamon Press, Oxford. pp. 367–374. doi:10.1016/B978-0-08-024928-5.50049-X.

Staples, J.F. 2016. Metabolic flexibility: Hibernation, torpor, and estivation. Compr. Physiol. **6**(2): 737–771. doi:10.1002/cphy.c140064. PMID:27065167.

Tower, J., and Arbeitman, M. 2009. The genetics of gender and life span. J. Biol. **8**(4): 38. doi:10.1186/jbiol141. PMID:19439039.

Turbill, C., Bieber, C., and Ruf, T. 2011. Hibernation is associated with increased survival and the evolution of slow life histories among mammals. Proc. R. Soc. B Biol. Sci. **278**(1723): 3355–3363. doi:10.1098/rspb.2011.0190. PMID:21450735.

Van Vuren, D. 1989. Effects of intraperitoneal transmitter implants on yellow-bellied marmots. J. Wildl. Manage. **53**(2): 320–323. doi:10.2307/3801130.

Webster, A.B., and Brooks, R.J. 1980. Effects of radiotransmitters on the meadow vole, *Microtus pennsylvanicus*. Can. J. Zool. **58**(6): 997–1001. doi:10.1139/z80-139. PMID:7000327.

Wheeler, H.C., and Hik, D.S. 2013. Arctic ground squirrels *Urocitellus parryii* as drivers and indicators of change in northern ecosystems. Mammal Rev. **43**(3): 238–255. doi:10.1111/j.1365-2907.2012.00220.x.

White, G.C., and Burnham, K.P. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study, **46**(sup1): S120–S139. doi:10.1080/00063659909477239.

Wilbur, S.M., Barnes, B.M., Kitaysky, A.S., and Williams, C.T. 2019. Tissue-specific telomere dynamics in hibernating arctic ground squirrels (*Urocitellus parryii*). J. Exp. Biol. **222**: jeb204925. doi:10.1242/jeb.204925. PMID:31515236.

Williams, B.K., Nichols, J.D., and Conroy, M.J. 2002. Analysis and management of animal populations. Academic Press, San Diego, Calif.

Williams, C.T., Barnes, B.M., Kenagy, G.J., and Buck, C.L. 2014*a*. Phenology of hibernation and reproduction in ground squirrels: integration of environmental cues with endogenous programming. J. Zool. **292**(2): 112–124. doi:10.1111/jzo.12103.

Williams, C.T., Wilsterman, K., Kelley, A.D., Breton, A.R., Stark, H., Humphries, M.M., et al. 2014*b*. Light loggers reveal weather-driven changes in the daily activity patterns of arboreal and semifossorial rodents. J. Mammal. **95**(6): 1230–1239. doi:10.1644/14-MAMM-A-062.

Williams, C.T., Wilsterman, K., Zhang, V., Moore, J., Barnes, B.M., and Buck, C.L. 2016. The secret life of ground squirrels: Accelerometry reveals sex-dependent

plasticity in above-ground activity. R Soc. Open Sci. **3**(9): 160404. doi:10.1098/rsos.160404. PMID:27703706.

Williams, C.T., Buck, C.L., Sheriff, M.J., Richter, M.M., Krause, J.S., and Barnes, B.M. 2017. Sex-dependent phenological plasticity in an arctic hibernator. Am. Nat. **190**(6): 854–859. doi:10.1086/694320. PMID:29166160.

Wilsterman, K., Buck, C.L., Barnes, B.M., and Williams, C.T. 2015. Energy regulation in context: Free-living female arctic ground squirrels modulate the relationship between thyroid hormones and activity among life history stages. Horm. Behav. **75**: 111–119. doi:10.1016/j.yhbeh.2015.09.003. PMID:26416501.

Wu, C.-W., and Storey, K.B. 2016. Life in the cold: Links between mammalian hibernation and longevity. Biomol. Concept. **7**(1): 41–52. doi:10.1515/bmc-2015-0032.

Young, R.C., Kitaysky, A.S., Haussmann, M.F., Descamps, S., Orben, R.A., Elliott, K.H., and Gaston, A.J. 2013. Age, sex, and telomere dynamics in a long-lived seabird with male-based parental care. PLoS One, **8**(9): e74931. doi:10.1371/journal.pone.0074931.

Zhang, V.Y., Williams, C.T., Palme, R., and Buck, C.L. 2020. Glucocorticoids and activity in free-living arctic ground squirrels: Interrelationships between weather, body condition, and reproduction. Horm. Behav. **125**: 104818. doi:10.1016/j.yhbeh.2020.104818. PMID:32698015.

Copyright of Canadian Journal of Zoology is the property of Canadian Science Publishing and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.