

# Plasticity and repeatability of activity patterns in free-living Arctic ground squirrels

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Social interactions can shape daily activity patterns, and this is an area of growing research interest. The propensity for individuals to be active at certain times of day may structure interactions with competitors and potential mates, influencing fitness outcomes. Aspects of daily activity such as timing of activity onset and offset exhibit within-individual repeatability, which raises the possibility that they may be subject to natural and sexual selection. This study used a biologging approach in free-living Arctic ground squirrels, *Urocitellus parryii*, to test the hypothesis that interactions between the sexes shape temporal patterns of daily activity. We predicted that males would become active earlier than females during the mating period, consistent with sexual selection on activity timing. We also examined repeatability in activity timing and how repeatability estimates are affected by sampling methodology. We deployed collar-mounted light loggers on ground squirrels and used timing of light transitions to determine daily onset and offset of above-ground activity. We observed 87 animals over 3 years, collecting over 7500 observations of daily activity. We found that daily activity timing had moderate (onset) to low (offset) adjusted repeatability. The difference in daily activity timing between the sexes varied seasonally: males remained active later than females during mating, while females initiated activity earlier and extended activity later during lactation. Adjusted repeatability estimates were sensitive to sampling methodology: they varied seasonally and declined with increased behavioural sampling. These results suggest that offset, not onset, may be shaped by sexual selection and that life history differences shape sex-dependent activity patterns in ground squirrels. We propose that activity onset may be under more strict circadian control than offset. This study suggests that researchers must consider seasonality and sampling design when estimating behavioural repeatability. Biologging could transform studies of individual variation by enabling high-frequency sampling of free-living animals.

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## INTRODUCTION

Recent reviews (Hau et al., 2017; Helm, Piersma, & Van der Jeugd, 2006) have called for greater attention to the way that timing structures biological communities, including within-taxon social interactions. While many studies have focused on the way that natural selection may shape timing decisions (Kronfeld-Schor & Dayan, 2003), less attention has been paid to the way that sexual selection may shape activity timing (Hau et al., 2017). There are numerous instances in which timing decisions may affect sexual

selection in free-living animals. Timing of sexual displays (intersexual selection) or of agonistic interactions between competitors (intrasexual selection) may influence which individuals have access to mates. Additionally, mate preference (intersexual selection) may fluctuate across the day, although this is not well studied.

Activity timing typically occurs on a diel (24 h) basis and results from the interplay of endogenous circadian clocks and direct responses to environmental cues. Even in high-latitude environments that experience periods of constant light and dark, there is evidence that at least some species (although not all) continue to exhibit 24 h activity cycles (Stelzer & Chittka, 2010; Swade & Pittendrigh, 1967; Ware et al., 2020; Wilson, Culik, Coria, Adelung, & Spairani, 1989; but see van Oort et al., 2005) and physiology (Ashley, Schwabl, Goymann, & Buck, 2013; Hau, Romero, Brawn, & Van'tHof, 2002; Silverin et al., 2009; Williams, Barnes, & Buck, 2012; Williams,

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Barnes, Yan, & Buck, 2017). Exhibiting diel patterns in activity and physiology can allow animals to exploit opportunities and avoid risks that occur on a predictable 24 h basis (Pittendrigh, 1993), and a few studies have demonstrated survival (DeCoursey, Walker, & Smith, 2000; Spoelstra, Wikelski, Daan, Loudon, & Hau, 2016) and reproductive (Greives et al., 2015) benefits for animals with a functional biological clock and/or an activity rhythm of 24 h.

While diel activity cycles are common within and across taxa, they are not expressed identically by all individuals. There are well-documented sex differences in activity timing. For example, female blue tits, *Cyanistes caeruleus*, start and end activity earlier than males (Schlicht & Kempenaers, 2020), while male great tits, *Parus major*, leave nestboxes earlier than females (Stuber, Dingemanse, Kempenaers, & Mueller, 2015). Reproductive male European ground squirrels, *Spermophilus citellus*, initiate activity earlier than females and nonreproductive males during mating (Everts, Strijkstra, Hut, Hoffmann, & Millesi, 2004). The fitness benefits of activity onset may also differ by sex. Male blue tits that rise early have more extrapair copulations (Poessel, Kunc, Foerster, Johnsen, & Kempenaers, 2006), a finding also shown in an experiment in male great tits (Greives et al., 2015); however, early rising female blue tits do not (Schlicht, Valcu, Loës, Girg, & Kempenaers, 2014). These findings suggest that in mating systems with male–male competition, onset and offset of activity timing within the day, and therefore circadian clocks, may be under sexual selection (Hau et al., 2017).

In addition to differing between the sexes, activity timing may also differ among individuals. Some individuals may consistently begin and end activity earlier in the day than others; these persistent individual differences in activity timing are called chronotypes. Chronotypes were first described in humans (summarized in Randler, 2014), then in laboratory animals (e.g. Labyak, Lee, & Goel, 1997), and only more recently in free-living systems. Chronotype studies in free-living animals are still relatively rare and are almost exclusively conducted in birds. These studies suggest that traits such as timing of dawn song (Murphy, Sexton, Dolan, & Redmond, 2008), sleep (Steinmeyer, Schielzeth, Mueller, & Kempenaers, 2010) and activity onset and offset (Dominoni, Helm, Lehmann, Dowse, & Partecke, 2013; Maury, Serota, & Williams, 2020; Schlicht et al., 2014; Schlicht; Kempenaers, 2020) show consistent individual differences (see Table 1).

While repeatability in daily activity and rest has been the focus of research on biological rhythms, over the last two decades repeatability in a broad range of traits has been the focus of research on animal behaviour, ecology, physiology and other fields seeking to incorporate individual variation into our understanding of biological systems (reviewed in Bell, Hankison, & Laskowski, 2009; Bolnick et al., 2011; Cauchoix et al., 2018; Taff, Schoenle, & Vitousek, 2018). This growth in research into trait repeatability has been accompanied by discussions about how repeatability estimates are affected by sampling methodology (Adolph & Hardin, 2007; Bell et al., 2009; Dingemanse & Dochtermann, 2013). Key decisions are debated, such as how many individual behavioural samples to use in repeatability estimates and how samples should be temporally distributed (Dingemanse & Dochtermann, 2013); however, collecting behavioural samples with high enough temporal resolution to address these questions using traditional observational methods remains a challenge.

We employed a biologging approach to study sex differences and repeatability in the timing of above-ground activity onset and offset in Arctic ground squirrels, *Urocitellus parryii*. Biologging allowed us to collect daily observations of activity timing in many individuals across months, and sometimes years, to build a robust data set with which to estimate repeatability and examine how it is affected by sampling decisions. Male Arctic ground squirrels are polygynous (Lacey, Wiczorek, & Tucker, 1997; Lacey & Wiczorek, 2001) and undergo a very brief and intense period of competition for mates and territories upon emergence from hibernation in the spring (Buck & Barnes, 2003; Carl, 1971; Lacey & Wiczorek, 2001). Females typically mate with multiple males on the day of peak receptivity, and research suggests that the first mate she copulates with is more likely to sire the majority of her offspring (Lacey et al., 1997; Lacey & Wiczorek, 2001). While the exact mechanisms that determine the relationship between courtship order and successful paternity are unknown, this is a system with high potential for sexual selection to shape activity timing. Consistent with the hypothesis that daily activity timing is subject to sexual selection, we predicted that males and females would differ in daily activity timing and that these differences would vary seasonally. Specifically, we expected that males would initiate activity earlier in the day than females during the brief and intense mating period, given that territorial defence and acquisition is associated with mating

**Table 1**  
Repeatability estimates for onset and offset of daily activity in literature

Species	Onset repeatability	Offset repeatability	Source
Blue tits, <i>Cyanistes caeruleus</i>	0.49 (breeding males)	0.58 (breeding males)	Schlicht & Kempenaers (2020)
	0.67 (wintering males)	0.79 (wintering males)	
	0.39 (breeding females)	0.29 (breeding females)	
	0.46 (wintering females)	0.37 (wintering females)	
	0.41 (winter and breeding both sexes)	0.38 (winter and breeding both sexes)	
	0.16–0.37 (within-years, breeding females)	N/A	
0.15 (across years, breeding females) <i>n.s.</i>		Steinmeyer et al. (2010) Schlicht et al. (2014)	
Dark-eyed juncos, <i>Junco hyemalis aikeni</i>	0.73 [95% CI: 0.67, 0.76] (incubating females)	N/A	Graham et al. (2017)
European blackbirds, <i>Turdus merula</i>	0.50 (urban)	0.49 (urban)	Dominoni et al. (2013)
	0.51 (forest)	0.65 (forest)	
European starlings, <i>Sturnus vulgaris</i>	0.22 (incubation)	0.11 (incubation) <i>n.s.</i>	Maury et al. (2020)
	0.36 (chick rearing)	0.18 (chick rearing)	
Great tits, <i>Parus major</i>	0.27 [95% CI: 0.02, 0.42] (incubating females)	N/A	Graham et al. (2017) Stuber et al. (2015)
	0.13 [95% CI: 0.10, 0.16] (wintering both sexes)	0.00 [95% CI: 0.00, 0.00] (wintering both sexes)	
Pine siskins, <i>Spinus pinus</i>	0.56 [95% CI: 0.38, 0.67] (nocturnal activity in migratory birds of both sexes)	NA	Rittenhouse et al. (2019)

*n.s.*: repeatability was not significant for studies that did not report confidence intervals in text.

opportunities and defence against extrapair copulation (Lacey & Wieczorek, 2001). We also predicted that Arctic ground squirrels would show repeatable within-individual variation in daily timing of activity, which is consistent with the existence of chronotypes that have been detected in other systems. Importantly, we also predicted that repeatability estimates would be sensitive to sampling decisions; specifically, that they would vary with season and sex and decrease with increased behavioural sampling.

## METHODS

### *Animals*

Arctic ground squirrels were studied across 3 years (2014–2016) at two field sites on the North Slope of Alaska: Atigun (68°27'N, 149°21'W; elevation 812 m) and Toolik Lake (68°38'N, 149°38'W; elevation 719 m). Detailed accounts of two sites have been published elsewhere (Sheriff et al., 2011; Williams et al., 2016). Briefly, Arctic ground squirrels hibernate for up to 8 months of the year (Buck & Barnes, 1999). Males terminate hibernation earlier than females and remain below ground for about 3 weeks at euthermic body temperatures while gonads develop and spermatogenesis is established before they emerge onto the surface (Williams, Barnes, Richter, & Buck, 2012a). In the second half of April and early May, females terminate hibernation and emerge almost immediately (Sheriff et al., 2011). Females achieve reproductive competence within days (Buck & Barnes, 1999), and males experience a period of intense scramble competition for access to females during the brief mating season (Buck & Barnes, 2003; Carl, 1971; Lacey & Wieczorek, 2001). Females mate with one to four males on the day of sexual receptivity (Lacey et al., 1997). Mating is typically complete by late April to early May (Buck & Barnes, 1999), and females gestate for approximately 25 days (Lacey, 1991) before giving birth. Offspring remain below ground for approximately 3.5 weeks after birth, and lactation ends at the end of June/early July, or about 1 week after young emerge above the surface (Lacey, 1991). Both sexes gain significant mass prior to hibernation (Buck & Barnes, 1999). Since sexes enter hibernation at different times, mass gain is observed across July into early August in females, and across August into September in males (Buck & Barnes, 1999; Sheriff, Fridinger, Barnes, & Buck, 2013). Prior to hibernation, males spend several weeks, beginning in mid-July (Lacey, 1991), caching food that they eat below ground the following spring during testicular recrudescence. Females do not cache food in their hibernacula (Buck & Barnes, 1999; Gillis, Morrison, Zazula, & Hik, 2005).

Ground squirrels were live-trapped near their burrows between 0800 and 2100 hours using carrot-baited Tomahawk traps (model numbers 103 and 104.5, Tomahawk Live Trap Co., Tomahawk, WI, U.S.A.) that were checked hourly. Squirrels were fitted with a light logger mounted on a custom collar (total device weight 0.3%–2.25% body mass) to determine timing of burrow use under 3–5% isoflurane anaesthesia (see Williams et al., 2014; Williams et al., 2016). Two types of loggers were used: BAS model MK7290 light loggers (1 g; Biotrack Ltd, Dorset, U.K.), which record light levels every 2 min, and Intigeo-C56 and C330 light loggers (1 g and 3 g; Migrate Technology Ltd, Cambridge, U.K.), which record light levels at 1 min or 5 min sampling intervals (see Supplementary Material). Squirrels were provided carrots, apples and/or Mazuri rodent chow (Mazuri Rodent Chow, Brentwood, MO, U.S.A.) in quantities commensurate with the duration of time they remained in captivity. After recovery from anaesthesia, they were returned to the site of capture within 1–24 h depending upon local weather conditions. Collar fit was evaluated any time that the animal was re-trapped, and light loggers were retrieved opportunistically at variable intervals from logger deployment. Battery life permitted

loggers to be redeployed for up to 2 years; in many cases squirrels were refitted with a second collar and logger when the first ceased to function. This allowed us to collect up to three consecutive years of data from the same individual, although most individuals had only 1 year of data due to natural mortality (males), recapture success (both sexes) and the removal of devices whose batteries were anticipated to fail during the winter hibernation (both sexes). Alaska Department of Fish and Game permitted work with animals under permits 14–074, 15–079, 16–074 and 17–100. The Institutional Animal Care and Use Committee (IACUC) of the University of Alaska Fairbanks approved this work under protocols 340270 and 864841.

### *Weather Data*

Hourly temperature, precipitation, wind speed and solar radiation data were collected at Atigun with a Hobo U30-NRC weather station (Onset Computer Corporation, Bourne, MA, U.S.A.). At Toolik, hourly weather data were collected courtesy of the Toolik Field Station Environmental Data Centre weather station (Environmental Data Center Team, 2017). All sensors used successfully collected data on 98.2% of days during our study. On select dates when one or more sensors at the Toolik Meteorological Tower malfunctioned, data were gap-filled using another meteorological tower at the station run by the Arctic Observatory Network, courtesy of Syn- donia Bret-Harte and Eugenie Euskirchen. Daily presence or absence of new snowfall at both sites was assessed using daily landscape scale images taken from cameras mounted on 10 m towers provided courtesy of the Toolik Field Station Environmental Data Centre (Environmental Data Center Team, 2017). Cameras captured data successfully on 93.4% of study days at Toolik and on 78.4% of study days at Atigun. When cameras malfunctioned, the Toolik Field Station's naturalist journal, which describes weather events, was used to determine whether it had snowed.

### *Statistical Analysis*

Light level records were trimmed to exclude data collected within 2 days of initial capture and on the day of logger download or retrieval. We restricted our analyses to samples taken between day 101 and day 244 of the year (11 April – 1 September in nonleap years), which is the period when we had at least one observation for both sexes. Data were processed to create a binary variable indicating that the squirrel was either exposed (0) or not exposed (1) to light for each sample (see Supplementary Material). Onset and offset of above-ground activity were calculated relative to 0122 hours, which was the time of minimum population level above-ground activity. For each date, the first record after 0122 hours that the squirrel had detectable light levels was defined as activity onset and the last record of light exposure within the subsequent 24 h was defined as activity offset.

We used R v.3.6.1 (R Core Team, 2016) with the 'brms' package (Bürkner, 2017) to build a Bayesian model of activity onset and offset. We modelled data with a student *t* distribution, to account for a fat-tailed distribution, with a random intercept for individual identity (ID), a spline for day of year fitted separately by sex, and fixed effects for sex (male or female), site (Atigun or Toolik), study year (2014, 2015 or 2016), daily average wind, temperature, solar radiation, presence of rain (yes/no) and presence of new snowfall (yes/no). An autoregressive process with a lag of one was included to account for autocorrelation in observations from the same individual across successive days within 1 year. All continuous independent and dependent variables were centred across individuals. We used default prior values in brms. Models were fitted with four chains, each sampling for 2000–4000 iterations with half of samples

devoted to warm-up. Upon inspecting model results, we observed unusual early onset (before 0500 hours) in a few cases. Therefore, we ran our model both including and excluding these observations and report results from full ( $N = 7879$ ) and restricted data sets ( $N = 7824$ ) (see [Supplementary Material](#)). We inspected trace plots for chain mixing, model output for divergent transitions and posterior predictive plots for model fit. Rhat values for all parameters in the fitted model were between 1.00 and 1.01. Results are reported as means with a 95% credible interval.

We also divided the restricted data set into subsets and modelled each subset to examine how sampling and modelling decisions affected repeatability estimates. Briefly, to see whether repeatability estimates varied seasonally, we divided the data from the restricted data set into nine 15-day windows across the active season (day of year 106–240). To examine how the number of observations per individual affected repeatability estimates, we used data collected in 2015 and selected the individuals for whom the largest number of daily observations had been collected. We further divided observations of these animals into data sets representing up to 5, 10, 20, 30, 40 and 80 observations per individual. We also split the restricted data set by sex and modelled each sex separately. These data sets were modelled using a similar procedure as the model described above (see [Supplementary Material](#)).

Output for each model was used to calculate adjusted repeatability values by dividing the variance attributable to individual ID by the sum of that quantity and residual model variance. This yielded an adjusted repeatability score because our models included fixed effects for weather covariates, which allowed us to account for extrinsic factors known to affect activity and to account for the fact that all individuals were not sampled every day. We followed [Nakagawa and Schielzeth \(2010\)](#) and did not use within-individual centering of fixed effects. Repeatability was calculated from the samples generated during model fitting, which allowed us to estimate a 95% credible interval.

## RESULTS

We observed onset and offset of activity in 87 individuals (50 females and 37 males). In the restricted data set, females were observed on 7–314 separate days (mean  $\pm$  SD =  $88 \pm 68$  days),

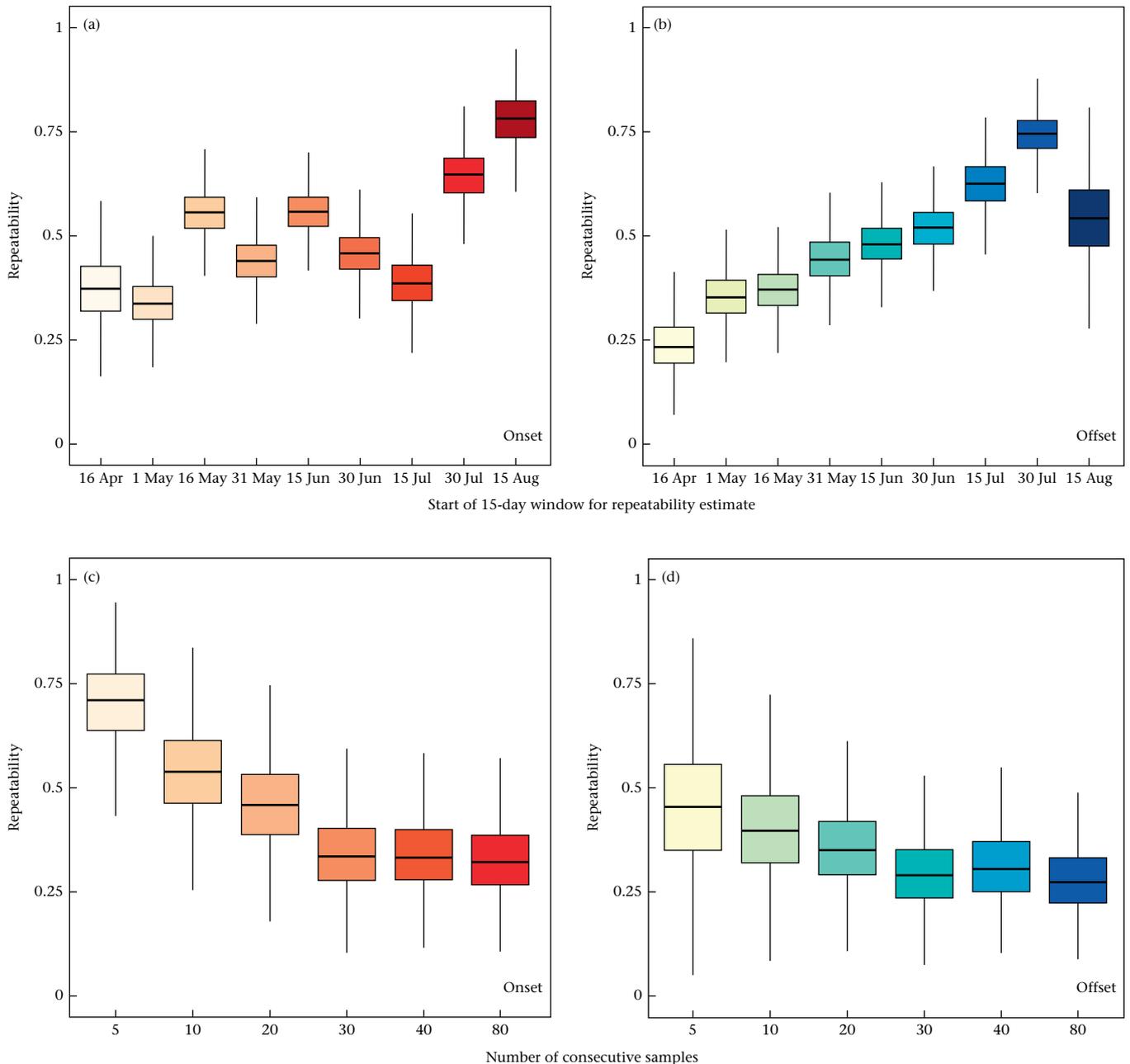
while males were observed on 3–265 separate days ( $93 \pm 58$  days). Most males and females were only observed in 1 year, although 19 females and 14 males were observed across 2 or more years. The restricted data set excluded 56 observations (see [Supplementary Material](#)), which were from animals that initiated activity unusually early before 0500 hours. These observations were overwhelmingly from females ( $N = 54$  observations) and were concentrated in the second half of June. This early rising behaviour was observed in 18 different females, most of whom only exhibited early rising on one occasion. However, four female squirrels exhibited this behaviour on 5 or more days. Below, we report detailed model results from analyses of the restricted data, which were highly similar to findings from the full data set. Results from analyses of the full data set can be found in the [Supplementary Material \(Figs S1, S2, Tables S4, S6, S7\)](#).

### *Influence of Sex, Seasonality and Number of Observations on Estimates of Adjusted Repeatability in Activity Onset and Offset*

Repeatability estimates for above-ground activity onset and offset were low to moderate and did not differ between calculations made from models of restricted and full data sets. Activity onset repeatability (0.26, 95% CI [0.20, 0.35]; [Table 2](#)) was higher than activity offset repeatability (0.12, 95% CI [0.06, 0.22]). Importantly, our models calculating repeatability estimates from different data subsets indicated that repeatability estimates of onset and offset were sensitive to sex, seasonality and number of behavioural samples ([Fig. 1, Table 2](#)). Repeatability estimates for males and females calculated separately differed from the overall estimates of repeatability from models of both sexes combined ([Table 2](#)). Onset was less repeatable in females (0.17, 95% CI [0.11, 0.25]; [Table 2](#)) than in males (0.31, 95% CI [0.21, 0.44]); however, there was no clear sex difference in offset repeatability. Unlike models of the combined data set, when data for each sex was modelled separately, there were no clear differences in the repeatability of onset and offset ([Table 2](#)). Repeatability in offset and onset fluctuated seasonally; however, the temporal change in estimates differed for the two measures ([Fig. 1a, b, Table 2](#)). Onset repeatability fluctuated across the early and midseason and increased at the end of the summer ([Fig. 1a](#)). Offset repeatability estimates indicated a gradual

**Table 2**  
Repeatability estimates reported as means  $\pm$  95% credible intervals for all models of activity onset and offset

Data modelled	Onset repeatability mean [95%CI]	Offset repeatability mean [95% CI]
<b>All days, both sexes</b>		
Restricted data set	0.27 [0.20, 0.35]	0.12 [0.06, 0.22]
Full data set	0.26 [0.20, 0.35]	0.12 [0.06, 0.22]
<b>All days, subset by sex</b>		
Females	0.17 [0.11, 0.25]	0.24 [0.17, 0.34]
Males	0.31 [0.21, 0.44]	0.28 [0.18, 0.41]
<b>Subset by season, both sexes</b>		
day of year 106–120	0.37 [0.23, 0.53]	0.24 [0.12, 0.39]
day of year 121–135	0.34 [0.23, 0.47]	0.36 [0.25, 0.48]
day of year 136–150	0.56 [0.45, 0.66]	0.37 [0.27, 0.49]
day of year 151–165	0.44 [0.33, 0.55]	0.45 [0.33, 0.56]
day of year 166–180	0.56 [0.46, 0.66]	0.48 [0.38, 0.59]
day of year 181–195	0.46 [0.35, 0.57]	0.52 [0.41, 0.63]
day of year 196–210	0.39 [0.27, 0.52]	0.62 [0.51, 0.74]
day of year 211–225	0.65 [0.52, 0.76]	0.74 [0.64, 0.83]
day of year 226–240	0.78 [0.64, 0.89]	0.54 [0.35, 0.73]
<b>Subset by number of samples per individual (collected on consecutive days), both sexes</b>		
5 samples	0.70 [0.48, 0.87]	0.45 [0.18, 0.73]
10 samples	0.54 [0.33, 0.75]	0.40 [0.19, 0.64]
20 samples	0.46 [0.27, 0.68]	0.36 [0.19, 0.57]
30 samples	0.34 [0.18, 0.55]	0.30 [0.16, 0.50]
40 samples	0.34 [0.19, 0.54]	0.31 [0.17, 0.52]
80 samples	0.33 [0.19, 0.53]	0.28 [0.15, 0.46]



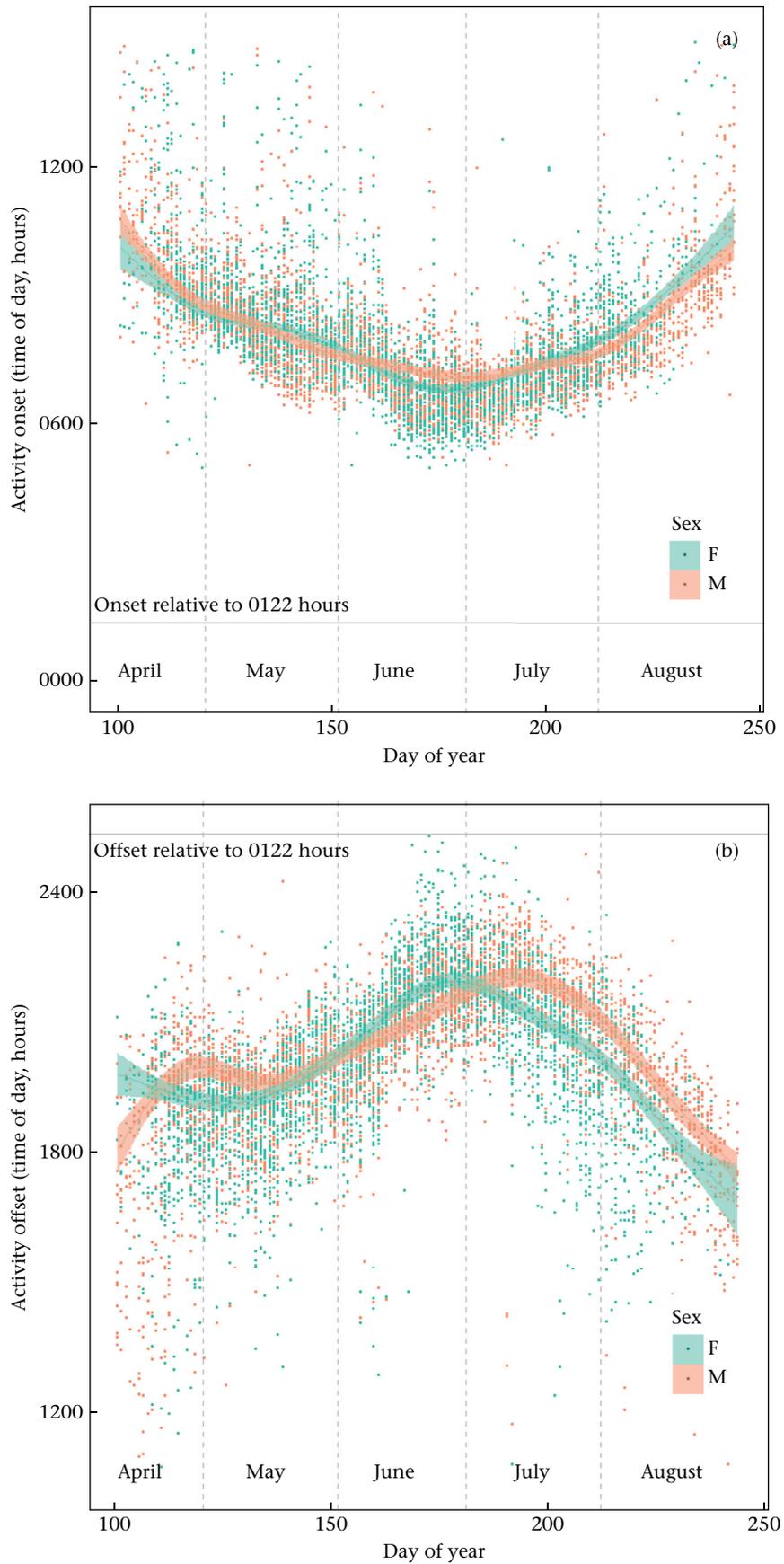
**Figure 1.** Onset (left) and offset (right) repeatability estimates calculated using data from different phases of the active season (a, b) and representing different number of samples (c, d). The thick black lines represent the median of each distribution, and the box represents the 25th and 75th percentiles. The whiskers represent  $\pm 1.5$  times the interquartile range.

increase across the season (Fig. 1b). Both onset and offset estimates appeared sensitive to the number of behavioural samples included in analyses: repeatability estimates appeared to decrease for both measures as the number of behavioural samples increased from 5 to 30, although this pattern was more pronounced for onset than for offset (Fig. 1c, d, Table 2). Repeatability estimates were similar as number of samples increased from 30 to 80 (Fig. 1c, d, Table 2).

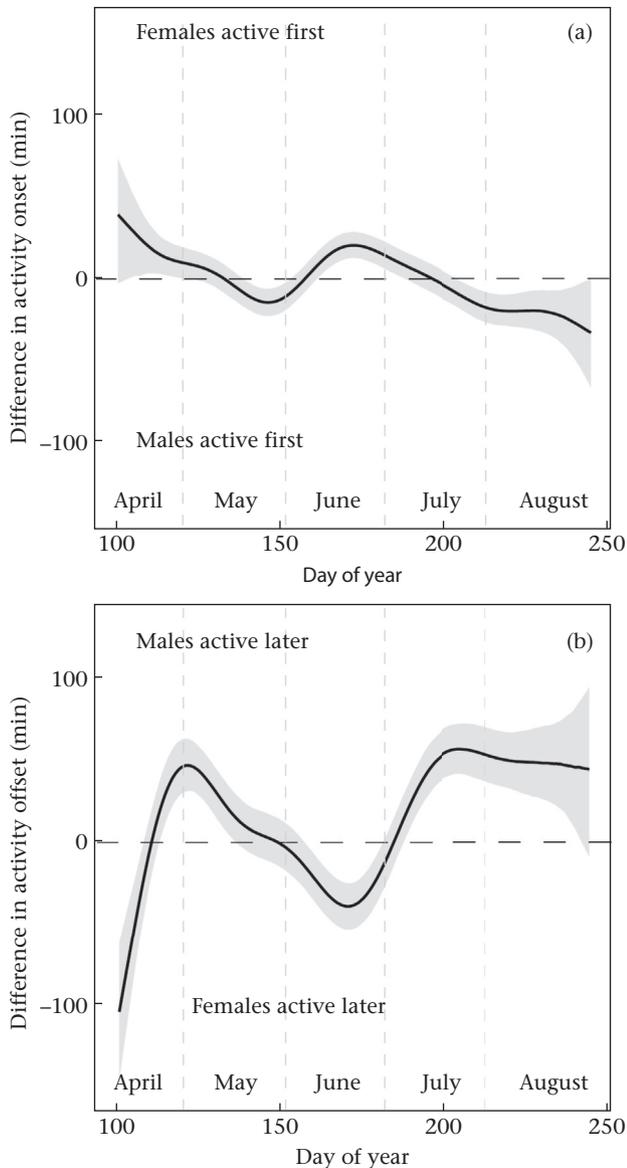
#### *Influence of Season and Sex on Activity Onset and Offset*

Both activity onset and offset showed seasonal variation. Activity onset patterns followed a U-shaped seasonal trajectory, while activity offset patterns followed an inverse U-shaped pattern. This suggests that onset was earliest in the middle of the season, which was also when offset was the latest. Across the spring and

summer active season, timing of activity offset fluctuated much more than timing of activity onset (Fig. 2, Supplementary Fig. S1). While males and females showed similar overall seasonal changes in activity onset and offset, there were still some sex differences in activity timing (Fig. 3, Supplementary Fig. S2). Models of activity onset (Fig. 3a, Supplementary Table S3) indicated that females began daily activity earlier than males in early April and again during late June and early July. Males were active earlier for a brief period at the end of May and then again from the end of July through August. Offset results indicated that females were active later than males during emergence from hibernation in mid-April and then again at the end of June (Fig. 3b, Supplementary Table S5). Males were active later than females from the end of April through mid-May, and then again in July and August (Fig. 3b, Supplementary Table S5).



**Figure 2.** Predicted seasonal changes in activity (a) onset and (b) offset in male and female Arctic ground squirrels under average/reference conditions from models of the restricted data set. The shaded region represents the 95% credible interval for mean estimates. Thirty-six points for onset occurring after 1500 hours and seven points for offset occurring prior to 1030 hours are omitted. In this system, mating occurs in late April/early May, parturition occurs in late May and lactation occurs through late June.



**Figure 3.** Differences in activity (a) onset and (b) offset between male and female Arctic ground squirrels predicted by models of the restricted data set. Differences are calculated from pointwise estimates of fitted model values for males and females under average/reference environmental conditions. The solid black line represents the mean value of the difference; the shaded region represents the 95% credible interval. In this system, mating occurs in late April/early May, gestation occurs in late May and lactation occurs through late June.

#### *Influence of Weather on Activity Onset and Offset*

Temperature, wind speed and solar radiation predicted variation in both onset and offset of activity while snow and rain predicted variation in offset only. Weather factors typically had a stronger effect on activity offset than on activity onset. As temperature increased, squirrels initiated activity above ground earlier ( $\beta = -2.73$ , 95% CI [-2.93, -2.53]; [Supplementary Table S3](#)) and exhibited activity later in the evening ( $\beta = 2.70$ , 95% CI [2.37, 3.04]; [Supplementary Table S5](#)). High levels of solar radiation delayed both activity onset ( $\beta = 0.07$ , 95% CI [0.06, 0.08]; [Supplementary Table S3](#)) and offset ( $\beta = 0.17$ , 95% CI [0.16, 0.19]; [Supplementary Table S5](#)). Overall, wind suppressed activity, with increasing wind speeds delaying onset in the morning ( $\beta = 0.78$ , 95% CI [0.31, 1.29];

[Supplementary Table S3](#)) and advancing offset in the evening ( $\beta = -8.74$ , 95% CI [-9.59, -7.87]; [Supplementary Table S5](#)). The interaction between temperature and wind speed did not predict variation in activity onset ( $\beta = 0.02$ , 95% CI [-0.06, 0.10]; [Supplementary Table S3](#)); however, the negative relationship between temperature and activity offset was enhanced at high wind speeds ( $\beta = 0.35$ , 95% CI [0.21, 0.49]; [Supplementary Table S5](#)). Presence of snow ( $\beta = 0.87$ , 95% CI [-2.18, 3.89]; [Supplementary Table S3](#)) and rain ( $\beta = 1.10$ , 95% CI [-0.41, 2.62]; [Supplementary Table S3](#)) did not predict activity onset; however, snow led to earlier offset ( $\beta = -10.53$ , 95% CI [-14.90, -6.26]; [Supplementary Table S5](#)) and rain led to later offset ( $\beta = 11.57$ , 95% CI [8.98, 14.26]; [Supplementary Table S5](#)).

#### **DISCUSSION**

Our results suggest that contrary to expectation, sex differences in activity offset, but not onset, may reflect sexual selection on activity timing. Male ground squirrels remained active later in the day than females during the mating period, potentially resulting from the late afternoon oestrus and copulation behaviour seen in this species ([Lacey et al., 1997](#)). Sex differences in activity timing at other times across the summer seem to reflect sexual dimorphism in life history and energetic demand. We also found that individuals exhibited circadian-phase preferences (i.e. chronotypes): onset had moderate within-individual adjusted repeatability while offset showed low adjusted repeatability and high sensitivity to fluctuations in weather conditions. We propose that this indicates that activity onset may be under more strict circadian control than offset. Importantly, our results also suggest that repeatability estimates are sensitive to basic sampling decisions such as what time of year to sample and how many behavioural samples to take. We suggest that researchers carefully evaluate these decisions when conducting studies of trait repeatability.

#### *Sex Differences in Activity Across the Season*

We anticipated that males would show earlier activity onset than females in late April and early May when competing for mates, as this pattern has been shown in other systems ([Everts et al., 2004](#)) and is consistent with expectations from sexual selection ([Hau et al., 2017](#)). Our results do not support this prediction and suggest that females, not males, show slightly earlier activity onset during mating, a difference found only in analyses of the restricted data set. However, during the mating period in late April, there were sex differences in activity offset: males typically remained active later than females. This is interesting because the only detailed account of mating behaviour in Arctic ground squirrels indicated that females exhibit behaviours consistent with oestrus on a single day at mid-afternoon (around 1500 hours) and that copulation takes place later that day (1700–2100 hours) ([Lacey et al., 1997](#)). Later activity offset during mating in late April and early May could allow males to gain additional copulation opportunities in the evening; thus, there seems to be potential for sexual selection on activity offset rather than on activity onset in the Arctic ground squirrel system.

Other differences in activity timing may be influenced by sex differences in energetic demand emerging from sexually dimorphic elements of life history. In June, females initiated above-ground activity earlier than males and also extended activity later into the evening than males, even in analyses of the restricted data set that removed 'outlier' observations. This is not surprising because in June most females are lactating and provide high levels of maternal care to offspring ([Lacey, 1991](#)). A doubly labelled water

study in golden mantled ground squirrels, *Spermophilus saturatus*, indicated that lactation is the period of highest energetic demand for females (Kenagy, Sharbaugh, & Nagy, 1989); in this species, mass specific metabolic rate of females during lactation is higher than that of males at any point in the year. Early onset of surface activity in females during June may reflect foraging to meet the energetic demands of lactation. A study of daily activity patterns in lactating red squirrels, *Tamiasciurus hudsonicus*, found that lactating females exhibit three peaks in activity across the course of the day, with high levels both early and late in the day (Williams et al., 2014). Lactating female skunks, *Mephitis mephitis*, also show earlier activity onset and later activity offset (Zhang, Williams, Theimer, & Buck, 2019). Similarly, female European ground squirrels (Everts et al., 2004) and golden hamsters, *Mesocricetus auratus* (Larimer et al., 2011) spend more time foraging during lactation, especially during late lactation immediately prior to weaning. While previous work using light loggers to describe activity patterns in Arctic ground squirrels has reported that females are active almost exclusively between 0600 hours and 2300 hours (Williams et al., 2014); this study detected activity between 2300 hours and 0600 hours and suggests that late night and early morning activity by female Arctic ground squirrels may be an uncommon, but potentially important, feature of this life history stage. Indeed, scattered reports of late night and early morning squirrel activity appear elsewhere in the literature (Long, Martin, & Barnes, 2005; Swade; Pittendrigh, 1967), although they are typically treated as aberrations. Similarly, one of the few studies to examine below-ground activity in Arctic ground squirrels with accelerometers suggests some below-ground activity by lactating females as well (Williams et al., 2016). While we are not proposing that female squirrel activity becomes arrhythmic during lactation, parental care has been shown to uncouple activity patterns from the underlying circadian rhythm in some avian species (Bulla et al., 2016; Steiger et al., 2013). Additionally, in the postreproductive period, our data indicate that males consistently initiate above-ground activity earlier and terminate above-ground activity later than females. Given that in this system only males cache food in the hibernaculum, male activity patterns during the mid and late summer may be driven by the need to forage for food used the following spring (Buck & Barnes, 1999; Gillis et al., 2005). Alternatively male activity may be associated with late-season territorial defence (Buck & Barnes, 2003). Females may also exhibit later activity offset in the very early spring when they are first emerging from hibernation; however, the sparse data for females at this time of year makes this finding tentative at best.

While sex differences in activity onset and offset fluctuated across the spring and summer, activity timing showed robust seasonal changes in both sexes after accounting for the impact of key weather variables (Fig. 2). For both sexes, activity onset was earliest and activity offset was latest in midsummer, while activity onset occurred later and offset occurred earlier at the beginning and end of the summer active season. While it is very common for diurnal animals at temperate latitudes to show seasonal changes in activity patterns, activity typically tracks sunrise and sunset, and seasonal changes are reported relative to light cues. The sun does not set at our study sites from late May through late July and the sun does not go more than six degrees below the horizon (end of civil twilight) from early May to mid-August. Given the absence of entraining sunrise and sunset cues, it is unclear what cues Arctic ground squirrels are using to guide seasonal shifts in activity timing and maintain entrained circadian rhythms of physiology and behaviour (Williams, Barnes, & Buck, 2012; Williams et al., 2017). It is notable, however, that day of year continued to explain variation in the timing of activity after controlling for weather parameters.

### *Individual Repeatability in Activity Patterns: General Patterns and Effects of Sampling Methodology*

Despite the many factors contributing to activity timing, there was still moderate adjusted repeatability in activity onset. Although offset had low adjusted repeatability, the confidence intervals on repeatability did not include zero. These adjusted repeatability scores are lower than other values reported in the literature for onset and/or offset of activity in most systems (Table 1). One possible explanation for this is that our analysis for repeatability, unlike many others, explicitly accounted for temporal autocorrelation in measurements, which is known to inflate repeatability estimates when left unaccounted for (Mitchell, Dujon, Beckmann, & Biro, 2019). Additionally, our data set encompassed many observations for each animal, including observations across multiple years for some, and meta-analyses suggest that repeatability of behaviour decays over time (Bell et al., 2009; Holtmann, Lagisz, & Nakagawa, 2017). For example, a study in female blue tits showed that emergence time was repeatable within years but not across years (Schlicht et al., 2014). Similarly, a study in fox squirrels, *Sciurus niger*, found that individuals did not exhibit consistent patterns of rising early or late across seasons, but did within seasons (Wassmer & Refinetti, 2019). Another possibility for our lower adjusted repeatability values is that onset and offset of activity are inherently more variable in an Arctic system, especially under conditions of constant light. Given that sunrise and sunset did not occur for most of our study period and we do not know what entraining cues Arctic ground squirrels use under continuous light conditions, we relied upon a seasonal spline to account for the variance in onset and offset behaviour attributable to changing seasonality. In all likelihood, this does not perfectly account for variance in activity timing that could be attributed to the zeitgeber for circadian activity in Arctic ground squirrels if it were known. Ultimately, given the large number of observations for most individuals in this multi-year study, the finding that these measures show any within-individual repeatability is notable.

The repeatability of within-individual variation in onset and offset of above-ground activity strongly suggests that Arctic ground squirrels have circadian chronotypes, which have been demonstrated in humans (Randler, 2014) as well as several avian species (Table 1). This is exciting because it opens the possibility of examining whether changes in social or environmental conditions lead to selection of particular chronotypes, although more work is needed to establish whether chronotype is a heritable trait. While our study cannot definitively assess whether individual differences in onset and offset reflect differences in the underlying biological clock, or individual differences in phenotypic plasticity in response to the environment, other studies have suggested that onset and offset differences are associated with underlying clock function (Spoelstra et al., 2016). A few studies suggest that individual variation in the circadian clock and/or daily activity timing may also be associated with differences in seasonal timing. Early chronotypes have been linked to earlier breeding in dark-eyed juncos, *Junco hyemalis aikeni*, and great tits (Graham, Cook, Needham, Hau, & Greives, 2017) and earlier nocturnal migratory behaviour in captive pine siskins, *Spinus pinus* (Rittenhouse, Robart, & Watts, 2019). In the future, it will be interesting to see whether daily chronotype is associated with variation in hibernation phenology.

The rich data set that we generated using a biologging approach also allowed us to show how sampling methodology affects repeatability estimates. We found that repeatability estimates varied across the season and decreased as the number of behavioural samples per individual increased. Interestingly, the seasonal patterns of repeatability in activity onset and offset showed different patterns: while activity onset estimates fluctuated across

a range of intermediate values, estimates of activity offset showed a gradual increase across the season from low repeatability in the spring to fairly high repeatability at the end of the summer. Few studies have investigated the effect of seasonality on repeatability estimates, although findings in some avian species also suggest that repeatability estimates may differ across life history stages (Table 1).

Our findings for both activity onset and offset indicate that repeatability declines with increased behavioural sampling: estimates of repeatability calculated from five behavioural samples had higher mean values but much higher uncertainty than estimates calculated from 30 or more behavioural samples. We are confident in this general pattern since we found similar decreases in repeatability for both activity onset and offset. This is consistent with meta-analyses suggesting that repeatability decays with greater temporal separation between samples (Bell et al., 2009; Holtmann et al., 2017); given our analytical approach, estimates that are calculated from a greater number of samples also represent samples that were taken across greater intervals of time. Notably, Bell et al. (2009) found that the number of samples taken per individual did not affect repeatability estimates. In general, studies on repeatability methodology assume that there are a fixed number of trials that a researcher may be able to conduct, and that the number of samples collected per individual trades off directly with the number of individuals sampled (Adolph & Hardin, 2007). Such papers typically advise sampling more individuals rather than increasing the number of trials per individual to increase statistical power, although when repeatability is low, increasing the number of trials may improve repeatability estimates (Adolph & Hardin, 2007; Dingemans & Dochtermann, 2013). Biologging is a powerful tool in repeatability studies because it facilitates high frequency sampling at lower time costs to the researcher; as such, it can be a tool to help researchers determine how sampling decisions affect repeatability estimates, especially for traits that may have lower repeatability values. For example, our data offer preliminary evidence that, at least in this system, repeatability estimates of activity timing stabilize after 20–30 samples per individual, when samples were collected over time spans of 20–30 days.

Finally, we show that basic modelling choices influence repeatability estimates. For example, offset repeatability estimates were much higher when the sexes were analysed using two separate models with a simple spline to account for seasonal trends than when they were modelled together with a seasonal spline  $\times$  sex interaction. While there is a rich body of literature assessing statistical approaches for calculating repeatability (Dingemans & Dochtermann, 2013; Mitchell et al., 2019; Nakagawa & Schielzeth, 2010; Wolak, Fairbairn, & Paulsen, 2012), we think it bears mentioning that repeatability estimates are inherently sensitive to sampling methodology and modelling decisions. As such, these decisions must be at the forefront of researchers' attention as they interpret the meaning of repeatability estimates.

#### *Effect of Weather on Activity Onset and Offset: Implications for Biological Clocks*

Our results agree with prior studies of Arctic ground squirrel behaviour that show weather affects the total amount of time that Arctic ground squirrels spend above ground each day (Long et al., 2005; Williams et al., 2014). For example, we found that activity onset was earlier and offset was later under high temperatures, which is consistent with previous work that found the overall length of daily activity was extended under higher temperature conditions (Long et al., 2005; Williams et al., 2014). Interestingly, the sensitivity of activity onset and offset to weather parameters differed: while presence of precipitation and snow did not predict

variation in activity onset, they did predict variation in offset. Similarly, the interaction of temperature and wind speed only predicted variation in activity offset. We propose that these findings indicate that onset of activity is under more strict control by the endogenous circadian clock and is less responsive to weather than offset. Preliminary support for this idea is found in the only other study to report activity onset and offset in a sciurid species across life history stages, which found that rain had a stronger effect on offset than on onset (Everts et al., 2004). This hypothesis is also supported by our finding that activity onset shows higher within-individual adjusted repeatability than offset in analyses of the entire restricted data set; although, this pattern was not seen when the sexes were analysed separately. Few studies of activity timing report repeatability for both onset and offset of behaviour (Table 1), so it is premature to determine how widespread this pattern is across taxa. Female European starlings, *Sturnus vulgaris*, have higher repeatability in onset than offset (Maury et al., 2020), while findings in other systems suggest comparable onset and offset repeatability (Table 1). Given the vast differences in sampling methodology across these studies, we think that future biologging studies collecting high frequency data can strengthen our evaluations of this question in other systems.

#### *Conclusions*

Using biologgers to measure diel activity patterns across months, and even years, we showed that both sexual selection and changing energetic costs associated with life history may shape activity timing in Arctic ground squirrels. By obtaining large numbers of observations of the same individuals across time, we were able to find evidence for chronotypes in Arctic ground squirrels and demonstrate that adjusted repeatability estimates in this system are sensitive to sampling decisions. We think that biologging provides a path forward for researchers interested in individual variation in behaviour, both by detecting behaviour of many individuals simultaneously in natural settings and by enabling researchers to collect rich data sets that mitigate bias in repeatability estimates introduced by sampling decisions.

#### **Declaration of Competing Interest**

None declared.

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#### **Supplementary Material**

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2020.09.007>.

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