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Territorial scent-marking and proestrus in a recolonizing wild Gray Wolf (*Canis lupus*) population in central Wisconsin

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Abstract

Gray Wolf (*Canis lupus*) uses scent-marking to communicate breeding status, dominance, and territorial boundaries. Despite its importance for reproduction and pack dynamics, information on scent-marking and proestrus in wild wolf populations is limited to a handful of locations. We estimated the rate of territorial scent-marking and the probability of proestrus in a recolonizing Gray Wolf population near the species southern range extent in eastern North America. An analysis of 221 pack-winters of tracking data show that the incremental addition of one wolf pack increased marking rates by 3.4%, whereas increasing the number of wolves in a pack decreased marking rates by 12.1%. Scent-marking rates subsequently increased from 1.9 times/km during recolonization to 3.0 times/km once the population was saturated. We observed evidence of proestrus from 19 December to 14 March with the highest probability of proestrus occurring around 6 February, after peak marking rates around 26 January. Repeated observations of bloody urinations within individual packs suggest proestrus averages 27.9 days. Our study reveals the role of population growth on territorial behaviours and provides a foundation for studies exploring the role of geographic and temporal variation on territorial and reproductive behaviours in wolves.

Key words: Behaviour; Gray Wolf; *Canis lupus*; proestrus; raised-leg urinations; recolonization; reproduction; scent-marking; territory

Introduction

Communication has long been recognized as an important process in the development and maintenance of social bonds and conveying breeding status. Gray Wolf (*Canis lupus*) uses scent-marking to facilitate pair bonding, synchronize courtship and mating, identify breeders and dominance, and maintain spatial boundaries between neighbouring territorial packs (Mech and Peters 1977; Rothman and Mech 1979; Harrington and Asa 2003; Mech and Boitani 2003). In breeding pairs, males typically raised-leg urinate (RLU) and females flex-leg urinate (FLU), although these animals also use standing-urination (STU) and squat-urination (SQU) postures (Asa *et al.* 1985). Immature offspring and subdominant males and females normally urinate by standing and squatting, respectively (Peters and Mech 1975; Mech and Peters 1977; Rothman and Mech 1979; Asa *et al.* 1985, 1990). The scent-marks of subordinates and offspring are interpreted as generally eliminatory, whereas scent-marks of the breeding pair (RLUs, FLUs) are associated with territorial defense

(hereafter, territorial scent-marks; Peters and Mech 1975; Mech and Peters 1977; Rothman and Mech 1979; Mech and Boitani 2003; Packard 2003; Mech and McIntyre 2022).

Territorial scent-marking appears to reflect perceived costs and benefits. Wolves tend to mark boundaries adjacent to other packs' territories more often than core areas, particularly where incursions have previously occurred (Peters and Mech 1975; Zub *et al.* 2003). In contrast, lone wolves, which may be more vulnerable than established packs, normally do not territorial scent-mark within saturated wolf populations (Peters and Mech 1975; Rothman and Mech 1979) but routinely territorial scent-mark in colonizing populations (Thiel 2000; Harrington and Asa 2003). Scratches associated with scent-marking are believed to express heightened assertiveness, possibly associated with breeding condition or territoriality (Peters and Mech 1975; Rothman and Mech 1979; Mech 2006).

Proestrus in mature female wolves is associated with bloody vaginal discharge and bloody urine can

be used to identify whether a female wolf is in proestrus (Seal *et al.* 1979; Asa *et al.* 1985, 1990; Asa 1995; Packard 2003). Proestrus reportedly lasts 14–45 days with the onset and duration varying by individual (Young and Goldman 1944; Seal *et al.* 1987; Asa *et al.* 1990). In captive wolves, bloody discharge lasts between 15.7 ± 4.2 SD and 27 ± 6.5 SD days (Young and Goldman 1944; Seal *et al.* 1979, 1987; Asa *et al.* 1990; Esquivel *et al.* 1993 as cited in Alonso-Spilsbury *et al.* 2006), with proestrus extending from December to March (Asa *et al.* 1990). Schmidt *et al.* (2008) reported evidence of proestrus in wild Gray Wolves from mid-January to mid-March, peaking in February.

Information on scent-marking behaviour and proestrus in wild wolves is limited to a handful of locations (Peters and Mech 1975; Rothman and Mech 1979; Zub *et al.* 2003; Schmidt *et al.* 2008). Previous studies have evaluated spatial variation in territorial and reproductive behaviours in saturated populations; studying territorial scent-marking in a recolonizing population provides a unique opportunity to assess how population growth influences these same behaviours.

We studied scent-marking and proestrus over 20 years in a recolonizing wild Gray Wolf population near the southernmost range edge in eastern North America. We document the type and seasonal span of scent-markings and bloody urinations, and estimate the effect of population size, pack size, and day-of-year on territorial scent-marking behaviours and the probability of proestrus of wolves in the Central Forest Region (CFR) of west-central Wisconsin, USA. Our study reveals new insights into the relationship between canid population growth and territoriality, and provides a basis for future research assessing both geographic and temporal variation of territorial and reproductive behaviours in wolves.

Methods

The 7155 km² study area is situated on a glacial lakebed centred around 44.3733°N, 90.4974°W. This region consists of sandy soils that support numerous extensive marshes and bogs as well as upland forests of oak (*Quercus* spp.), pine (*Pinus* spp.), and aspen (*Populus* spp.). Wolves were extirpated from the area following European colonization and began recolonizing in the early 1990s (Thiel 1993). The wolf population initially increased from eight wolves in three packs in 1995 to 135 wolves in 32 packs in 2012, before stabilizing at about 100–150 wolves in 26–36 packs (Figure 1). Average road density in the CFR is 1.29 km/km², however, wolf packs have established territories with an average road density between 0.84 and 1.00 km/km² (Thiel *et al.* 2009; Simpson 2019). For a more detailed description of the study area, see Thiel *et al.* (2009) and Simpson (2019).

Data collection

Winter track surveys were conducted by trained staff and citizen volunteers following snowfall between the winters of 1994–1995 and 2017–2018 (Thiel *et al.* 2009; Wydeven *et al.* 2009; Thiel 2018). Each winter, trackers searched for wolf sign along plowed roads and trails by driving slowly within designated survey blocks. Data collected included date, distance driven, wolf pack identity, the number of wolves counted and lengths of wolf trails followed,
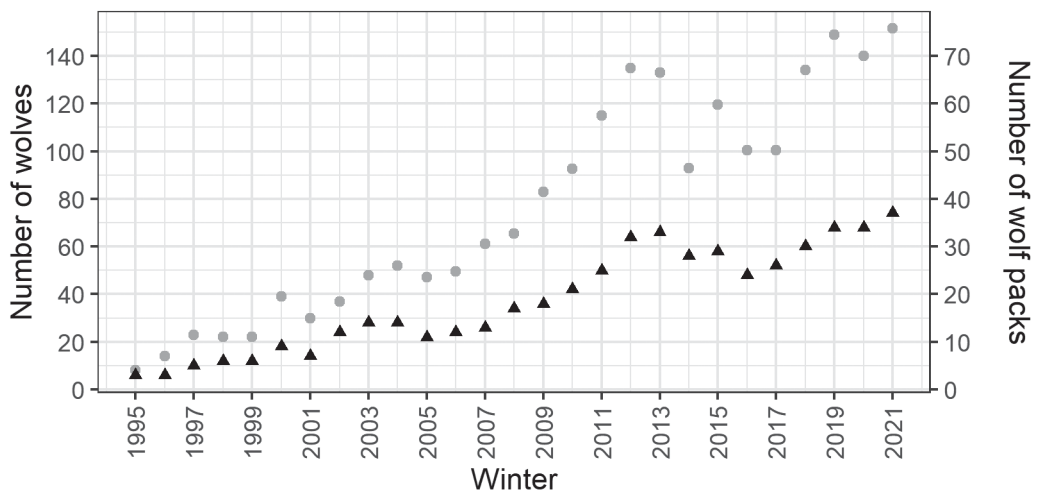

FIGURE 1. The number of Gray Wolf (*Canis lupus*) in the Central Forest Region, Wisconsin, USA based on data from the Wisconsin Department of Natural Resources. The number of packs is shown as black triangles and the number of wolves is shown as grey dots.

and the number and types of scent-marks encountered (Wydeven *et al*. 2009). Scent marks were identified by inspecting the position of wolf tracks relative to the urine. For example, urine is projected lateral to the direction of travel with one hind leg raised during RLU and projected down with one hind leg slightly raised during FLU. Neither hind leg is raised during SQU or STU, however, the hind legs are spread substantially wider than the body during the former but not the later (Asa *et al*. 1985). The presence of blood in the urine, evidence of a sexually mature female in proestrus (Peters and Mech 1975; Rothman and Mech 1979; Harrington and Asa 2003; Schmidt *et al*. 2008; Wydeven *et al*. 2009), was also recorded.

We summarized 20 years of winter-track survey data supplied by R.P.T. and three individuals who coordinated volunteers on behalf of the Wisconsin Department of Natural Resources. These records extend from November 1996 to February 1999, and from January 2002 to March 2018. Early winter data collection declined as the study progressed, so we restricted our study to data collected after 14 December. To compare our surveys to previous studies, we considered RLU, double raised-leg urinations (RLU^2), RLU with scratches, and RLU^2 with scratches as territorial scent-marks. Wisconsin winter-track surveys report FLUs as RLUs because the two scent marks are difficult to distinguish in some conditions, so our analyses include territorial scent-marks from both sexes. Bloody urine can occur in either territorial scent-marks or in eliminatory SQU, so we considered both as evidence of proestrus. Each encounter of a contiguous wolf trail segment was defined as an event in which the number of scent-marks was recorded by type. We assigned a tracking distance of 0.16 km in events where wolves merely crossed a road.

Statistical analyses

We estimated the rate of territorial scent-marks using a Poisson process model:

$$N_{it} \sim \text{Poisson}(\lambda_{it}) \cdot f_{it}$$

where N_{it} is the number of territorial scent-marking behaviours along path i on day t. The number of events is related to how far wolves were tracked so we included log(km) as an offset term (f_{it}) so that the estimated rate parameter $\log(\lambda_{it})$ represents the

average number of events/km of wolf-tracking effort. We also included a random intercept for survey block to account for correlated error structure that can arise from repeated measures of packs within an area. We evaluated seven models reflecting our expectation that territorial scent-marks could be related to the number of wolves in an event, the number of packs in the CFR, and day-of-year. Mid-winter pack sizes in the Upper Great Lakes region range from 2.7 to 5.5 wolves (Beyer *et al*. 2009; Erb and DonCarlos 2009; Thiel *et al*. 2009; Wydeven *et al*. 2009). Only 20 events (3%) recorded more than five wolves so we assigned all tracks ≥5 wolves a value of 5 to prevent overfitting. Statistical models were estimated by maximum likelihood methods using the "glmmTBM" package in R 4.0.5 (Brooks *et al*. 2017; R Core Team 2021). The most parsimonious model was identified using AIC (Akaike 1973).

Second, we tested evidence for a seasonal peak in proestrus using a binomial model:

$$S_{it} \sim \text{Binomial}(p_{it}).$$

We considered each individual urination an event, so the estimated parameter logit(p_{it}) represents the average probability that a territorial scent-mark or SQU contained blood. Urinations associated with the same animal are more likely to be similar to one another than we would expect at random, so we included a random intercept for survey block. We evaluated models reflecting no relationship, a linear relationship with time, a polynomial relationship with time, and the number of packs in the CFR. Statistical models were estimated using the beta-binomial distribution in "glmmTBM" (Brooks *et al*. 2017), which reduces to the binomial model when the number of trials per sample is one. We identified the most parsimonious model using AIC.

Results

Seventy-three volunteers drove 26 213 km over the 20-year period, resulting in 221 pack-winters of data. A total of 1301 territorial scent-marks were recorded along 642 km of wolf trails and accumulated 562 sample events (Table 1). Naïve winter marking rates averaged 2.3 marks/km (range 0–20). Due to monitoring protocols, all wolf trails were associated with

TABLE 1. Territorial scent-marks and squat urinations by type along 642 km of Gray Wolf (*Canis lupus*) tracks in the Central Forest Region, Wisconsin, USA.

	RLU	RLU^2	RLU with Scratch	RLU^2 with Scratch	SQU	Total
No blood	663	419	97	42	80	1301
Blood	49	30	1	3	7	90
Total	712	449	98	45	87	1391

Note: RLU = raised-leg and flexed-leg urinations, RLU^2 = double raised-leg and flexed-leg urinations, SQU = squat-urination.

at least one road and longer track segments often crossed multiple roads.

In winter, the average number of territorial scent-marks/km was related to the number of wolves in a pack, number of packs in the CFR, and day-of-year (Table 2). The most parsimonious model indicates that wolves were expected to mark an average of 2.4 times/km (range 0.9–4.6). The incremental addition of one wolf reduced territorial scent-marks/km by 12.1% ($P < 0.01$; Figure 2a) and the incremental addition of one wolf pack increased scent-marks/km by 3.4% ($P < 0.01$; Figure 2b; Table 3). We explored

different sine waves and found that the average rate of territorial scent-marks in the most parsimonious model peaked around 26 January.

Volunteers recorded 90 bloody urinations in 66 sampling events (Table 1) between 19 December and 14 March (Figure 3). Repeated observations of bloody urinations in single winters were observed within six packs over seven winters. The length from onset to end averaged 27.9 ± 18.9 SD days ($n = 7$; range 8–58 days). Our data indicated that proestrus peaked around 6 February (Figure 4) and was unrelated to the number of packs (Tables 2 and 3). We observed seven

TABLE 2. Model selection for territorial scent-marking (TSM) rates and proestrus in Gray Wolf (*Canis lupus*), in the Central Forest Region, Wisconsin, USA. Covariates include the number of wolves in an event (wolf), number of packs in the study area (packs), and number of days since 1 December (days). Territorial scent-marking was modeled as a Poisson process, whereas proestrus was modeled as a binomial process. The number of variables (K), AIC, difference between AIC values ($\Delta AICc$), and AIC weights (w) are provided for each model.

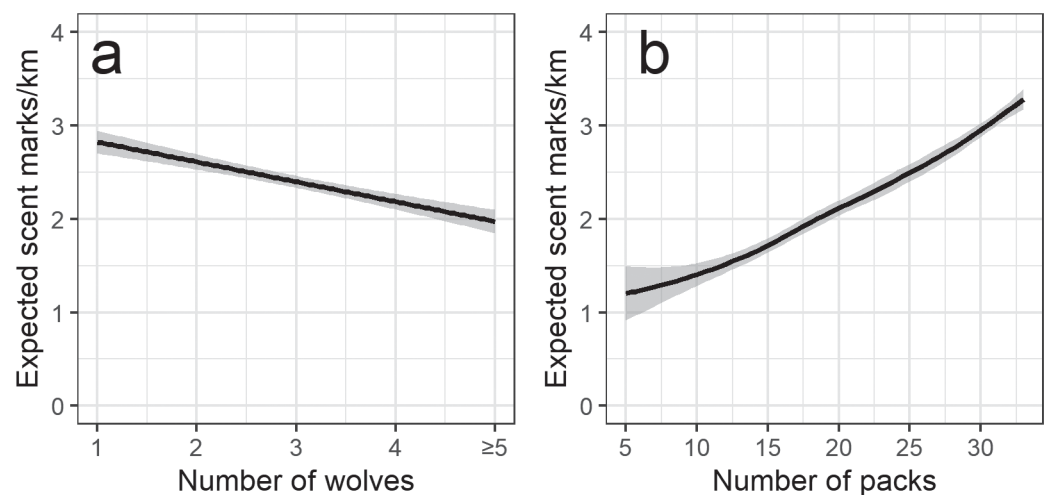| Model	Covariates	K	AIC	ΔAIC	w
TSM	wolf + packs + sine(day)	5	2513.8	0.0	0.94
	wolf + packs	4	2519.2	5.4	0.06
	packs + sine(day)	4	2533.2	19.4	0.00
	packs	3	2535.6	21.8	0.00
	wolf + sine(day)	4	2569.3	55.5	0.00
	wolf	3	2580.5	66.7	0.00
	sine(day)	3	2584.0	70.2	0.00
	null	2	2592.0	78.2	0.00
Proestrus	day + day^2	5	666.5	0.0	0.81
	sine(day)	4	670.0	3.5	0.14
	null	3	672.9	6.4	0.03
	packs	4	674.3	7.8	0.02

FIGURE 2. The mean rate of territorial scent marks/km by Gray Wolf (*Canis lupus*) from December to March in relation to a. pack size and b. number of packs in the study area. The estimated mean and 95% CI are shown in a black line and grey shading, respectively.

TABLE 3. Most supported mixed-effects models relating territorial scent-marking rates (TSM) to the number of Gray Wolves (*Canis lupus*) in a tracking event (wolf), the number of packs in the study area (packs), and relating the probability of proestrus to the number of days since 1 December (days). The estimated variance (σ) associated with the random intercept is shown for each model.

Model	Parameter	Estimate	SE	z value	P (>|z|)
TSM	Intercept	0.3725	0.1460	2.5507	0.011
	wolf	−0.1138	0.0247	−4.6104	< 0.001
	packs	0.0333	0.0044	7.6401	0.008
	sine(day)	0.0858	0.0321	2.6718	< 0.001
	σ	0.0694			
Proestrus	Intercept	−2.7339	0.1163	−23.5154	< 0.001
	scale(day)	8.8446	4.4992	1.9658	0.049
	scale(day)^2	−12.1534	4.9185	−2.4710	0.014
	σ	< 0.001			
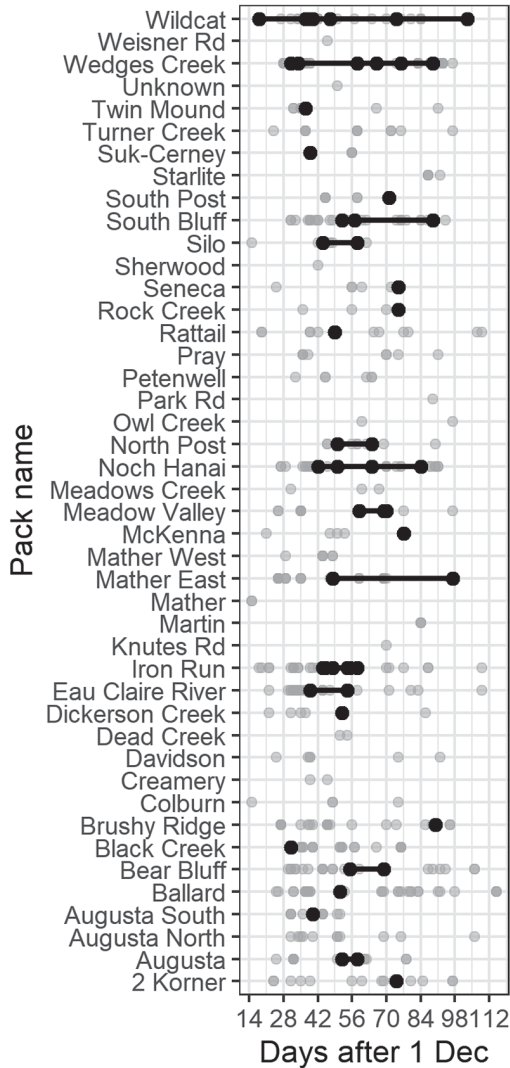
SQU with evidence of proestrus (Table 1). The ratio of SQU to territorial scent-marks was similar where proestrus (8.4%) was evident and when it was not (6.4%). We saw no evidence that the rate of SQU/km increased with pack size ($P = 0.272$).

Discussion

Territorial scent-marking peaked in the third week of January, which is earlier than reported by Zub *et al.* (2003) and by Peters and Mech (1975) who reported peaks in late February at latitudes about 8° and 3° farther north than our study area, respectively. The number of territorial scent-marks increased during recolonization, with an average expected rate of 1.9 marks/km (range 0.9–3.6) during the recolonization phase and 3.0 marks/km (range 1.3–4.6) once saturated. These are similar to midwinter rates reported in Poland (1.2–3.0 marks/km; Zub *et al.* 2003; Bojarska *et al.* 2020), Minnesota (1.7–3.4 marks/km; Peters and Mech 1975), and Manitoba (1.2–1.7 marks/km; Paquet 1991). Scent-marking rates are often higher along roads (Rothman and Mech 1978; Stępniak *et al.* 2020) but volunteers did not collect detailed spatial information relating wolf trails to roads, so we could not reliably assess the role of roads on territorial behaviour.

We found that wolves increased scent-marking in response to population growth, independent of pack size. Previous studies indicate that wolves increase marking in potential conflict areas (Peters and Mech 1975; Zub *et al.* 2003). Territorial scent-marking and

FIGURE 3. The occurrence of proestrus in territorial scent marking Gray Wolf (*Canis lupus*) from 14 December to 26 March by wolf pack. Black dots are scent markings with evidence of proestrus, black lines are the first and last date proestrus was observed in the same pack, and grey dots are sampling effort.
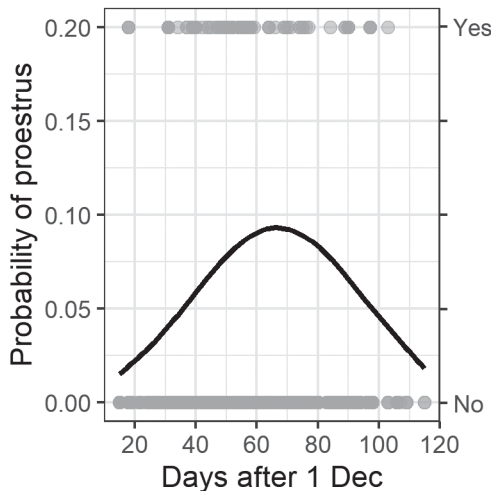
FIGURE 4. The mean probability of proestrus in Gray Wolf (*Canis lupus*) from 14 December to 26 March. The estimated mean is shown in a black line and the raw observations show whether individual scent-marks contained blood.

other olfactory cues might convey information on the size of wolf packs occupying territories or their willingness to defend a territory. This is important information to convey in maintaining competitive spaces because superior pack numbers, in addition to presence of males and older individuals, led by dominant individuals often sway outcomes in intra-pack aggressive encounters (Cassidy *et al*. 2015, 2017). Our study shows that wolf packs living in saturated landscapes invest more energy defending territories, whereas those that live in unsaturated landscapes can reallocate that energy to other pursuits. We speculate that the higher rates observed among newly forming pairs in a saturated wolf population arises from their need to be assertive because most pairs in such situations must usurp space from the interstitial areas between existing pack territories (Rothman and Mech 1979). Additional research would be required to assess the relationship between resource availability, pack formation, pack size, and scent marking.

Our findings are consistent with studies showing marking rates initially decline with increasing pack size (Peters and Mech 1975; Zub *et al*. 2003) and then increase as pack size exceeds five individuals (Peters and Mech 1975; Paquet 1991). We posit that the initial decline occurs because small packs need to mark assertively to usurp or maintain space while avoiding physical confrontation, whereas the subsequent increase may be related to pack composition. Territorial scent-marking is associated with dominant individuals (98%; Peterson *et al*. 2002) and small packs often consist of only two breeding adults and their pups. Be-

cause RLU first occurs during puberty, which typically occurs at 22 months old (Ranson and Beach 1985; Asa and Valdespino 1998), large packs may simply have more adults that are physiologically and behaviourally equipped to mark territory than smaller packs.

The observed season of bloody urinations (19 December to 14 March) compares favourably with those reported in Minnesota (4 January to 24 February; Rothman and Mech 1978) and Poland (12 January to 22 March; Schmidt *et al*. 2008). Proestrus in several central Wisconsin wolf packs spanned an average of 27.9 days and peaked in early February, which is consistent with observations in both captive and wild wolves (Seal *et al*. 1979, 1987; Asa *et al*. 1990; Esquivel *et al.* 1993 as cited in Alonso-Spilsbury *et al.* 2006). However, the mechanisms driving variability among individuals, neighbouring packs, and populations remain elusive. Reproductive phenology in wolves is positively correlated with lower latitudes, lower elevations, warmer summers, and warmer winters (Mech 2002; Joly *et al*. 2018; Mahoney *et al*. 2020), which are often associated with increased primary and secondary productivity. There is variable support for latitudinal gradients in ungulate reproduction across species and scales (Sigouin *et al*. 1997; Stoner *et al*. 2016; Neumann *et al*. 2020), indicating that geographic variation in wolf reproduction is not strongly linked to ungulate parturition. Wolves in western North America delayed denning after years with high primary productivity and high fall and winter precipitation but did not adjust denning dates over an 18-year period when start of the growing season advanced 14.2 days (Mahoney *et al*. 2020). That wolves fail to synchronize reproduction with spring onset suggests that breeding behaviour is highly conserved and that other processes or cues stimulate proestrus in female wolves (e.g., photoperiod or winter body condition). We speculate that reproductive phenology varies according to long-term patterns in resource availability and suggest that relating geographic and interannual measures of prey availability and body condition to proestrus, breeding, denning, and reproductive success may shed light on reproductive mechanisms in canids.

Author Contributions

Acknowledgements

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