




# Disentangling direct and indirect determinants of the duration of maternal care in brown bears: Environmental context matters

Joanie Van de Walle<sup>1</sup>  | Andreas Zedrosser<sup>2,3</sup> | Jon E. Swenson<sup>4</sup>  | Fanie Pelletier<sup>1</sup> 

<sup>1</sup>Département de biologie & Centre for Northern Studies, Université de Sherbrooke, Sherbrooke, QC, Canada

<sup>2</sup>Department of Natural Sciences and Environmental Health, University of South-Eastern Norway, Bø, Norway

<sup>3</sup>Institute of Wildlife Biology and Game Management, University of Natural Resources and Life Sciences, Vienna, Austria

<sup>4</sup>Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway

## Correspondence

Joanie Van de Walle

Email: joanie.van.de.walle@usherbrooke.ca

Andreas Zedrosser

Email: andreas.zedrosser@usn.no

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## Abstract

1. The duration of maternal care, an important life-history trait affecting population dynamics, varies greatly within species. Yet, our understanding of its predictors is limited, mostly correlative and subject to misinterpretations, due to difficulties to disentangle the role of maternal- and offspring-related characteristics.
2. We conducted path analysis on a dataset including 217 brown bear litters captured over a 29-year period in two populations in Sweden ('North' and 'South') facing contrasting environmental conditions to identify and quantify the causes of variation in the duration of maternal care (1.5 or 2.5 years).
3. We showed that the causal determinants of the duration of maternal care were context-dependent. Contrary to their expected central role in the determination of the duration of maternal care, yearling mass and its direct determinants (i.e. litter size and maternal mass) were only important in the North population, where environmental conditions are harsher and the cost of extended maternal care presumably higher. In the South, the duration of maternal care was not caused by yearling mass nor any maternal or litter characteristics. Extension of maternal care may thus result from factors independent from maternal and offspring condition in the South, such as an artificial hunting-induced selection for longer maternal care through the legal protection of family groups.
4. Our results provide an important contribution to our very limited knowledge of the direct and indirect determinants of the duration of maternal care and highlight the importance of accounting for the environmental context when assessing maternal reproductive tactics.

## KEYWORDS

brown bear, harvest, maternal care, path analysis, weaning age

## 1 | INTRODUCTION

Parental care refers to all parental behaviours yielding short- and/or long-term benefits to offspring in terms of growth, survival and reproduction (Clutton-Brock, 1991; Smiseth et al., 2012). Through the improvement in offspring fitness, care can also contribute to the inclusive

fitness of parents (Hamilton, 1964). However, the time and energy spent, and risk incurred, by parents while providing care (i.e. parental expenditure; Clutton-Brock, 1991) can be high and reach a level where it entails fitness costs (i.e. parental investment; Trivers, 1972). Natural selection should thus favour optimal levels of parental care maximizing offspring fitness while limiting parental fitness costs.

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When the costs of parental care outweigh their benefits, care should terminate and offspring be weaned (Davies et al., 2012; Trivers, 1974; Williams, 1966). In mammals, where parental care is provided almost exclusively by females (Clutton-Brock, 1991) and mostly takes the form of milk provisioning (Gittleman & Thompson, 1988), weaning is typically attained when offspring can survive on a milk-free diet (Borries et al., 2014). However, in species where other forms of care can also be provided (e.g. protection, teaching and assistance; Clutton-Brock, 1991) after nutritional independence, the total duration of maternal care may better reflect maternal expenditure. Moreover, in several species, females resume their reproductive activities only once maternal care ceases (Borries et al., 2014). Therefore, the duration of maternal care is directly linked with inter-birth intervals and reproductive rates and ultimately population dynamics (Van de Walle et al., 2018); thus, identifying its determinants is important from both ecological and management perspectives.

The duration of maternal care varies greatly between and within mammals. For example, lactation ranges from only 4 days in the hooded seal *Cystophora cristata* (Bowen et al., 1985) to up to 8 years in the African elephant *Loxodonta africana* (Lee & Moss, 1986). At the intraspecific level, empirical studies also report large variations in the duration of maternal care, ranging from days (e.g. harbour seal *Phoca vitulina*; Bowen et al., 2001), months (e.g. African leopard *Panthera pardus*; Balme et al., 2017) and even years (e.g. African elephant; Lee & Moss, 1986). Despite having the potential to affect long-term reproductive success and fitness of individual females (Balme et al., 2017; Van de Walle et al., 2018), our knowledge of the causal mechanisms leading to variation in the duration of maternal care is surprisingly limited.

Lee et al. (1991) showed in a comparative analysis that offspring age and mass at weaning are correlated across species, with offspring being weaned at the threshold mass of about four times their neonatal mass. Despite its interspecific focus, these findings suggest flexibility in the duration of maternal care, depending on offspring body condition, at the intraspecific level (Lee, 1996). Early weaning should be advantageous for females in good condition, which may wean offspring in good condition quickly and resume reproduction sooner (Lee et al., 1991), thereby increasing lifetime reproductive success (Fairbanks & McGuire, 1995). In less favourable conditions, females may face challenges in acquiring sufficient resources for optimal offspring growth and may either abandon offspring to allocate in their own maintenance or continue maternal care to improve offspring mass and survival prospects (Balme et al., 2017; Bowen et al., 2001; Lee et al., 1991; Lee & Moss, 1986; Trillmich, 1986). Maternal and offspring conditions should thus play a central role in determining the duration of maternal care (Lee et al., 1991); however, their relative importance may change in different environmental contexts.

Empirical studies have shown that the duration of maternal care can correlate with both maternal and offspring traits, such as condition (Trillmich, 1986), maternal age and experience (Bowen et al., 2001; Lonsdorf et al., 2019), litter size (König & Markl, 1987; Lee, 1996) and offspring sex (Lee & Moss, 1986). However, all of these traits can correlate with offspring mass, and their effect on the duration of maternal

care could be indirect. For instance, females with more reproductive experience and in better body condition have more resources to allocate to offspring growth (Georges & Guinet, 2000), leading to shorter maternal care (Lee et al., 1991). Litter size is typically linked with offspring mass, due to the trade-off between offspring size and number (Charnov & Ernest, 2006), which might explain why offspring from larger litters are weaned later (König & Markl, 1987). In polygynous species, where allocation in male offspring can be more beneficial compared to female offspring (Trivers, 1972), males may attain their optimal weaning mass later (Trillmich, 1986). Therefore, the role of maternal and offspring characteristics may be intertwined and there is a need to disentangle their direct and indirect contributions to the duration of maternal care.

Based on data collected over 29 years from 217 brown bear *Ursus arctos* litters in Sweden, our general objective was to identify and quantify the determinants of the duration of maternal care. More specifically, we aimed at (a) identifying the factors correlated with the duration of maternal care, (b) quantifying their direct and indirect causal contributions and (c) comparing their effects between two study populations experiencing contrasting environmental conditions. First, we investigated which maternal (i.e. maternal mass, age and parity status) and litter (i.e. yearling mass, litter size and sex ratio) characteristics could explain variation in the duration of maternal care. We expected a correlation between the duration of maternal care and both yearling mass and litter size (Dahle & Swenson, 2003a). Second, using path analysis, we tested and compared seven competing causal hypotheses to identify the direct and indirect determinants of the duration of maternal care. Generally, we expected a strong causal relationship between yearling mass and the duration of maternal care. Building on this, we tested six hypotheses: (1) maternal and litter characteristics have an indirect contribution through their effects on yearling mass; (2) maternal and litter characteristics affect the duration of maternal care both directly and indirectly and (3–6) maternal characteristics indirectly affect the duration of maternal care through their direct effects on litter characteristics. We also tested the alternative hypothesis (7) of no causal link between yearling mass and the duration of maternal care. Whereas in the second step we tested for a general causal pattern, in the third step we tested the causal hypotheses in two separate Swedish populations (North and South). In the North, climate is harsher and population density is lower compared to the South (Zedrosser et al., 2006). Due to the different environmental contexts, we expected different causal structures in the two populations. Specifically, because of the harsher climatic conditions in the North and the presumably higher cost associated with extended maternal care, we predicted offspring and maternal characteristics may be stronger predictors of a female's decision to continue maternal care there.

## 2 | MATERIALS AND METHODS

### 2.1 | Study species and data collection

The brown bear is a solitary, sexually dimorphic species, with males larger than females both as yearlings and adults (Dahle et al., 2006; Steyaert et al., 2012). In Scandinavia, females give

birth to one to four cubs in January and lactate in their winter den until den emergence in mid-April (Friebe et al., 2014; Manchi & Swenson, 2005). Females provide care (mostly lactation and protection) throughout the cubs' first year (at this stage cubs are referred to as 'cubs-of-the-year') and family groups hibernate together the following winter. After den emergence the second year, females either separate from their now yearlings, or continue maternal care for an additional year (cubs then are 2-year-olds; Dahle & Swenson, 2003a). Total duration of maternal care thus varies from 1.5 to 2.5 years (Van de Walle et al., 2018) and is correlated with yearling mass and litter size (Dahle & Swenson, 2003a).

We used data collected in a long-term monitoring program of brown bears in two populations (600 km apart) in Sweden. The first population (North) is located in Norrbotten County, northern Sweden (~67°N, 18°E), and the second (South) in Dalarna and Gävleborg counties, south-central Sweden (~61°N, 14°E). The North area is characterized by a mountainous landscape with deep valleys, and the South by a rolling landscape. Bear density is ~11 bears/1,000 km<sup>2</sup> in the North and ~30 bears/1,000 km<sup>2</sup> in the South (Støen et al., 2006). Mean temperatures in January and July are -13°C and 13°C, respectively, in the North, and -7°C and 15°C in the South. In the North, snow cover lasts from early October to late-May with a vegetation period of about 110–130 days, whereas snow cover lasts from late-October to early May with a vegetation period of about 150–180 days in the South (Zedrosser et al., 2006).

Hunting is allowed in the fall throughout Sweden and is regulated through regional quotas. Hunters with hunting rights and a weapon legal for big game hunting can kill any bear, except mothers and their dependent cubs of any age, which have been provided legal protection since 1986. In the South, legal hunting pressure is very high (~30% of marked bears die annually from hunting in recent years), which provides a survival advantage to females providing longer maternal care despite the associated reproductive costs (Van de Walle et al., 2018).

We used data from 1991 to 2011 (North) and 1990 to 2019 (South). Females were captured and chemically immobilized by darting from a helicopter in mid-April to mid-May (Arnemo et al., 2011). Family break-up occurs in May–July (Dahle & Swenson, 2003b), thus characteristics measured at spring capture should be representative of cues used by females to base their decision regarding separation from their yearlings. At capture, bears were equipped with a VHF (prior to 2003) or a VHF/GPS (after 2003) collar, which allowed relocation for observations and recaptures. For ethical reasons, cubs-of-the-year were not captured. Females were captured every second year and/or when with yearling cubs and were measured and weighed with a spring scale (to the nearest 0.5 kg). Once captured, individual yearlings were also weighed, and their sex was determined. For females followed since birth, age was known; for others, a vestigial premolar tooth was extracted for age determination (Matson

et al., 1993). Our dataset did not comprise any females giving birth after 26 years, thus we do not expect reproductive senescence (onset at 27 years in brown bears; Schwartz et al., 2003) in our study populations. Female reproductive state (solitary or with dependent cubs, regardless of their age) was determined through visual observations from a helicopter or the ground three times annually and their parity status (primiparous or multiparous) was determined from monitoring history. Because captures usually occurred within 2 weeks (Dahle et al., 2006), maternal and yearling mass were not adjusted for capture date. Yearling litter size ranged from 1 to 4, but due to few litters of 4 ( $n = 3$ ), we pooled litter sizes of 3 and 4 for further analyses. Litters where not all yearlings were measured ( $n = 15$ ) were removed from analyses. Analyses were conducted on litters rather than on individual yearlings, as all yearlings in a litter separate from their mother simultaneously (Dahle & Swenson, 2003b).

## 2.2 | Factors influencing the duration of maternal care

We constructed generalized linear mixed effects models using R package `LME4` (Bates et al., 2015) with 'duration of maternal care' as the response variable and maternal (maternal mass, age and parity status) and litter (average yearling mass, litter size and sex ratio) characteristics as explanatory variables. Duration of maternal care was treated as a binomial process ( $0 = 1.5$  years and  $1 = 2.5$  years). Using data from the North and South populations, we compared 24 candidate models (Table 1). The first six models contained only single variables: maternal mass (continuous; in kg), maternal age (continuous; in years), maternal parity status (categorical: primiparous or multiparous), yearling mass (continuous; average mass (kg) of yearlings in a litter), litter size (continuous; from 1 to 3 and 4) and sex ratio (continuous; proportion of males). Then, we constructed five additional models based on biologically relevant combinations of variables: maternal experience (maternal age, parity status), litter composition (litter size, litter sex ratio), maternal characteristics (maternal mass, age, parity status), litter characteristics (yearling mass, litter size, sex ratio) and a global model (all variables included). To account for potential population-specific effects, we added an interaction term with 'population' to all variables in all the above-mentioned models, which resulted in 11 additional models. Finally, we also added a model including only a population effect and a null model (intercept only), which resulted in a total of 24 models. As random intercepts, we included maternal identity to account for pseudoreplication and period (2 levels variable: period 1 = 1990–2004; period 2 = 2005–2019) to account for potential temporal effects in our sample in all models. All VIFs (variance inflation factor) were  $<3$ , suggesting that collinearity was not problematic. Correlation plot for the model variables is provided as

**TABLE 1** Candidate generalized mixed effects models constructed to determine variables affecting the duration of maternal care (response variable) in Scandinavian brown bears in Sweden from 1990 to 2019. All models included maternal identity and period (period 1: 1990–2004; period 2: 2005–2019) as random intercepts. Presented in the table for each model are the number of parameters ( $K$ ), the difference in AIC value corrected for small sample with the best performing model ( $\Delta\text{AICc}$ ) and model weight ( $\text{AICc}_w$ ). The best model is presented in bold. In models with a '\*Population', an interaction was included between population (North and South), and all the variables included in the model. See Section 2.2 for a description of the models

Model	$K$	$\Delta\text{AICc}$	$\text{AICc}_w$
<b>Litter size*Population</b>	<b>6</b>	<b>0.00</b>	<b>0.52</b>
Litter characteristics*Population	10	2.22	0.17
Yearling mass*Population	6	2.35	0.16
Litter composition*Population	8	4.02	0.07
Population	4	5.68	0.03
Maternal age*Population	6	7.67	0.01
Litter size	4	8.25	0.01
Maternal mass*Population	6	8.65	0.01
Sex ratio*Population	6	9.36	0.00
Maternal parity status*Population	6	9.70	0.00
Litter composition	5	9.85	0.00
Global*Population	16	11.32	0.00
Global	9	11.50	0.00
Litter traits	6	11.57	0.00
Maternal experience*Population	8	11.89	0.00
Maternal characteristics	6	12.57	0.00
Maternal characteristics* Population	10	13.53	0.00
Maternal age	4	14.91	0.00
Maternal mass	4	15.14	0.00
Maternal experience	5	15.63	0.00
Yearling mass	4	16.07	0.00
Null	3	16.11	0.00
Sex ratio	4	18.01	0.00
Maternal parity status	4	18.12	0.00

Supporting Information S1. Proportions of litters separated after 1.5 and 2.5 years of maternal care in each population and year are presented as Supporting Information S2. For each model, we extracted the difference of its Akaike's information criterion value corrected for small sample size ( $\text{AICc}$ ; Burnham & Anderson, 2002), compared to the best performing model ( $\text{AICc} = 0$ ) in our model set, along with its  $\text{AICc}$  weight ( $\text{AICc}_w$ ). For the best model, we estimated the proportion of variance explained by fixed and the combination of fixed and random effects, using marginal and conditional delta  $R^2$  (Nakagawa et al., 2017) with the R package MuMIn (Barton, 2019).

## 2.3 | Path analysis

We aimed to disentangle the causal relationships between maternal and litter characteristics and the duration of maternal care using path analysis. Path analysis, a generalization of structural equations modelling (SEM), allows the inclusion of nonlinear relationships between variables, nested structures and non-Gaussian data distributions (Shipley, 2000). SEM and path analysis are sensitive to the ratio of variables in relation to the sample size (Shipley, 2000). Therefore, to remain within the recommended ratio of 5–20 observations per path considered in our hypotheses (Petraitis et al., 1996), we only retained the four explanatory variables that performed best, based on AIC, in the first step. We specified seven causal hypotheses in the form of directed acyclic graphs (DAGs; Figure 1) and tested independence claims between variables not linked by an arrow in the DAGs using d-separation (Shipley, 2013). For each d-separation claim, we estimated the probability of absence of correlation between variables when controlling for their hypothetical causal parents ( $p$ ; null probability), where  $p > 0.05$  suggests d-separation. We assumed a Gaussian distribution for maternal mass, maternal age and yearling mass, and Poisson and binomial distributions for litter size and the duration of maternal care respectively. All models included maternal identity nested in population and period (period 1: 1990–2004; period 2: 2005–2019) as random factors. We combined null probabilities for each d-separation claim using Fisher's  $C$  statistic (Shipley, 2013), given by Equation 1.

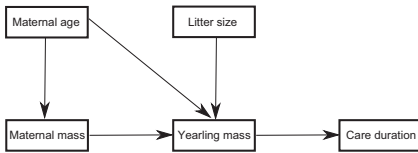
$$C = -2 \sum_{i=1}^c \ln(P_i). \quad (1)$$

A given DAG was accepted if the Fisher's  $C$  statistic followed a chi-squared distribution with  $2c$  degrees of freedom ( $c$  is the number of independence claims tested). For each DAG, we calculated its corresponding  $\text{AICc}$  using Equation 2 provided in Shipley (2013):

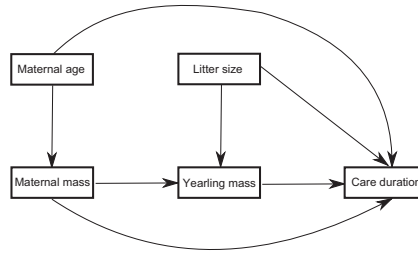
$$\text{AICc} = C + 2K \left( \frac{n}{n - K - 1} \right), \quad (2)$$

where  $C$  is the  $C$  statistic,  $K$  is the total number of maximum likelihood estimates from all mixed effects models included in the DAG and  $n$  is the sample size. We selected the accepted DAG with the lowest  $\text{AICc}$  value to estimate relationships within the DAG. Direct contributions were estimated from slope coefficients along a direct path (e.g.  $A \rightarrow C$ , with  $A$  being the direct cause of  $C$ ), whereas indirect contributions were estimated by multiplying all the slope coefficients from the single arrows along an indirect path (e.g.  $A \rightarrow B \rightarrow C$ , with  $A$  indirectly causing changes in  $C$  through its direct effect on  $B$ ). Finally, because a different causal structure may explain the duration of maternal care between populations, we also tested the seven hypothetical causal structures for each population separately. Random factors in those population-specific models were maternal identity and period.

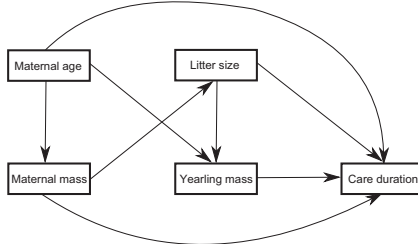
## Hypothesis #1



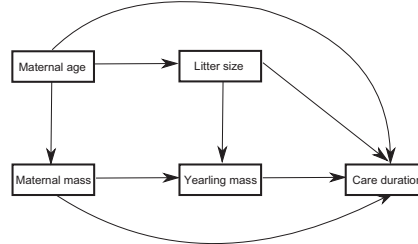
## Hypothesis #2



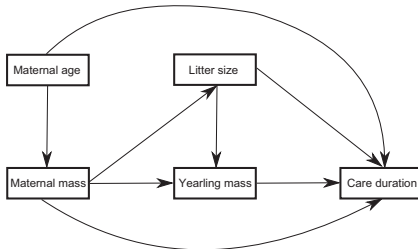
## Hypothesis #3



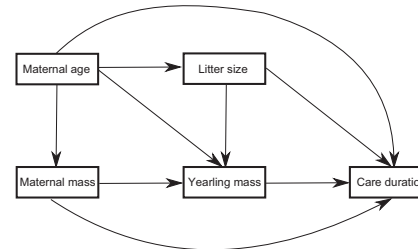
## Hypothesis #4



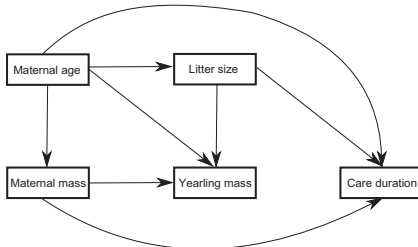
## Hypothesis #5



## Hypothesis #6



## Hypothesis #7



**FIGURE 1** Proposed hypotheses of causal structures to explain variation in the duration of maternal care in Scandinavian brown bears, 1990–2019

### 3 | RESULTS

#### 3.1 | Factors influencing the duration of maternal care

Our dataset included 217 yearling brown bear litters in both populations. For 15 litters, parity status of mothers was unknown and omitting those litters resulted in a sample size of 202 (North: 51; South: 151) litters from 93 (North: 31; South: 62) females. The best model explaining variation in the duration of maternal care included only litter size in interaction with population (Table 1). Marginal and conditional delta  $R^2$  were 0.16 and 0.52 respectively. All models including the interaction term with population (except model for maternal characteristics) outperformed their simplified version (i.e. models including the same variables without the interaction term), which indicated that the effects of the variables tested may differ between populations (Table 1). Models containing the single variables maternal

mass, maternal age, litter size and yearling mass all performed better (albeit only slightly better, except for litter size) than the null model, suggesting these variables may be important in explaining the duration of maternal care. In contrast, models including the single variables sex ratio and maternal parity status did not outperform the null model (Table 1).

#### 3.2 | Path analysis

The variables litter sex ratio and maternal parity status were omitted in the next step, as models including their single effects did not outperform the null model and even in interaction with population, those two variables were outperformed by the remaining four variables. We thus retained two maternal (maternal age and maternal mass) and two litter (litter size and yearling mass) characteristics in our causal hypotheses (Figure 1). Because our analyses excluded

maternal parity status, we considered the full dataset of 217 litters (North:  $n = 55$ , South:  $n = 162$ ).

When combining data from both populations, only hypotheses #6 and #7 were not rejected, with hypothesis #7 having the lowest AICc value (Table 2a). Based on hypothesis #7, we detected a direct contribution of litter size, maternal age and maternal mass to yearling mass (Figure 2; Supporting Information S3); yearlings were lighter if they were in larger litters and if their mother was older, but were heavier if their mother was heavier. Maternal age directly and positively affected maternal mass and thus also contributed indirectly to yearling mass ( $\beta$  through indirect path = 0.169). Our best model (#7) did not include a direct effect of yearling mass on the duration of maternal care. Instead, the duration of maternal care was directly and positively (and independently of yearling mass) affected by litter size (Figure 2). Indeed, the odds of continuing maternal care increased by a factor 2.17 for each additional yearling in a litter (Figure 3a).

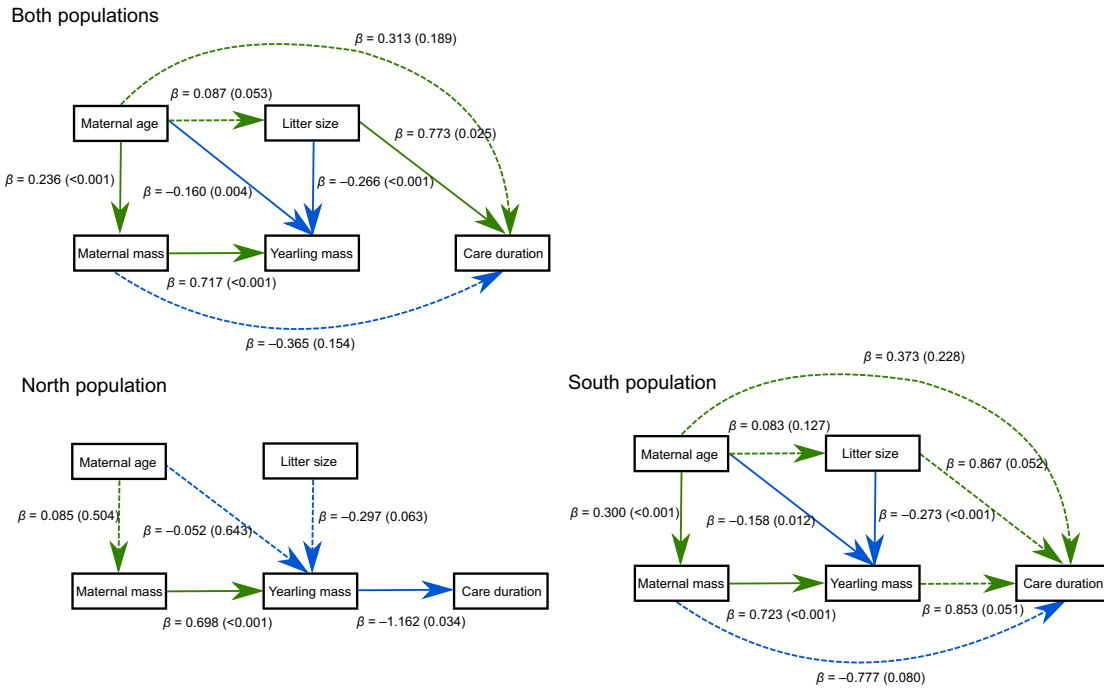
The variable selection in the first step indicated that the determinants of the duration of maternal care may differ between populations, providing support for also conducting path analyses of the duration of maternal care in the North and the South separately. The best causal structure differed between populations (Figure 2). In the North, the best causal structure was hypothesis

#1 (Table 2b). We detected a positive effect of maternal mass on yearling mass: yearlings were heavier if their mother was heavier. We also detected a tendency ( $\beta = -0.297$ ,  $p = 0.063$ ) for litter size to affect yearling mass (Figure 2; Supplementary Information S3). Yearling mass had a strong negative effect on the duration of maternal care: the odds of continuing maternal care decreased by a factor 3.2 per each increase of 1 kg in the average mass of yearlings within a litter (Figure 3b). Yearlings appeared to be weaned after 1.5 years of maternal care only if their weight was above 15 kg (Figure 3b). Maternal mass, through its direct effect on yearling mass, also indirectly and negatively affected the duration of maternal care ( $\beta$  through indirect path =  $-0.811$ ), with the odds of continuing maternal care decreasing by a factor 2.3 per each 1 kg increase in maternal mass. In the South, the best causal structure was hypothesis #6 (Table 2c). Yearlings were heavier if their mother was younger and heavier, and if they were in smaller litters (Figure 2; Supporting Information S3). Also, older females were heavier. However, we found only a tendency for the duration of maternal care to be affected by litter size ( $\beta = 0.867$ ,  $p = 0.052$ ; Figure 3c) and yearling mass ( $\beta = 0.853$ ,  $p = 0.051$ ; Figure 3d). No maternal characteristics contributed directly or indirectly to the duration of maternal care in the South (Supporting Information S3).

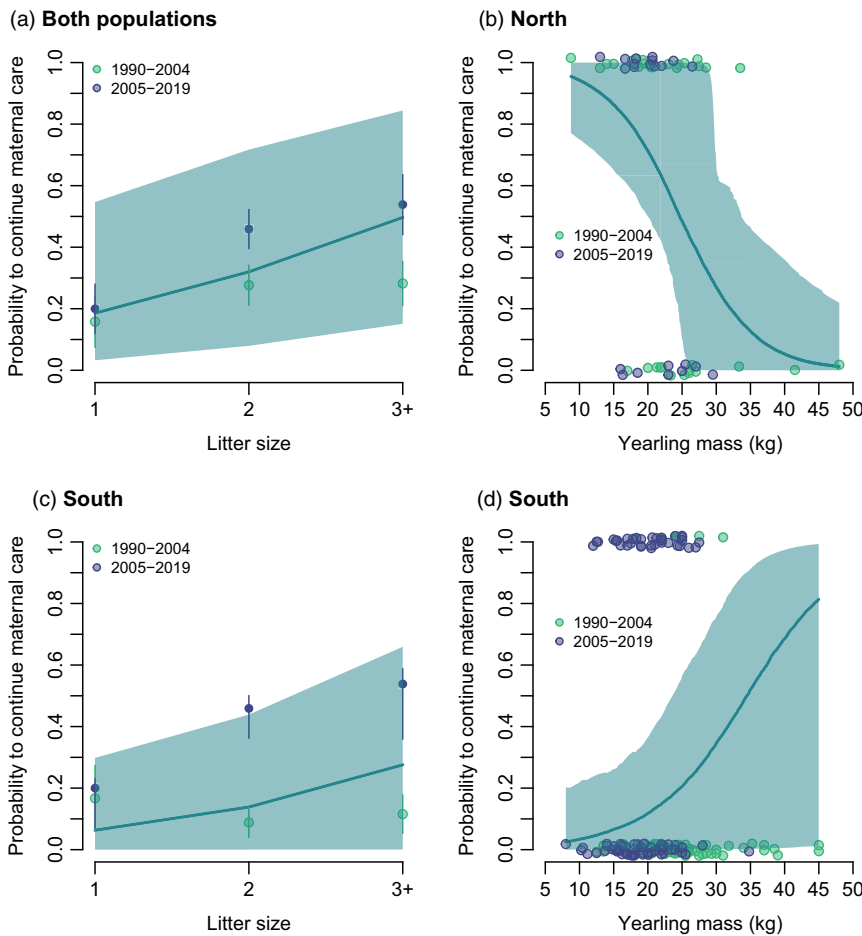
**TABLE 2** Results from tests of d-separation claims and AICc for the seven hypotheses of causal structures (DAGs) explaining the duration of maternal care in Scandinavian brown bears from (a) both populations (North, South) in Sweden from 1990 to 2019, (b) the North population from 1991 to 2011 and (c) the South population from 1990 to 2019. Marginal and conditional delta  $R^2$  are calculated based on the parametric model explaining the duration of maternal care. The best models are in bold

Hypothesis	Fisher's C	df	p-value	AICc	$R_m^2$	$R_c^2$
(a) Both populations						
1	33.46	10	<0.001	63.54	0.02	0.42
2	33.03	6	<0.001	67.75	0.07	0.47
3	132.92	4	<0.001	177.20	0.07	0.47
4	15.29	4	0.004	59.57	0.07	0.47
5	31.55	4	<0.001	75.83	0.07	0.47
6	2.96	2	0.281	49.69	0.07	0.47
7	<b>3.19</b>	<b>4</b>	<b>0.526</b>	<b>47.48</b>	0.07	0.47
(b) North population						
<b>1</b>	<b>17.29</b>	<b>10</b>	<b>0.068</b>	<b>55.80</b>	<b>0.22</b>	<b>0.40</b>
2	15.07	6	0.020	61.39	0.31	0.63
3	44.49	4	<0.001	109.20	0.31	0.63
4	4.63	4	0.327	69.34	0.31	0.63
5	14.57	4	0.006	79.28	0.31	0.63
6	0.51	2	0.776	70.51	0.31	0.63
7	6.92	4	0.140	71.63	0.17	0.46
(c) South population						
1	21.70	10	0.017	52.55	0.005	0.340
2	20.79	6	0.002	56.54	0.067	0.395
3	70.23	4	<0.001	116.18	0.067	0.395
4	10.98	4	0.027	56.94	0.067	0.395
5	19.98	4	0.001	65.94	0.067	0.395
<b>6</b>	<b>2.13</b>	<b>2</b>	<b>0.344</b>	<b>50.73</b>	<b>0.067</b>	<b>0.395</b>
7	8.27	4	0.082	54.23	0.039	0.353





**FIGURE 2** The best of the proposed hypothetical causal structures explaining variation in the duration of maternal care in both populations of Scandinavian brown bears as well as in the North and South populations, separately. Path coefficients are presented along with their associated *p*-values in parenthesis, with solid and dashed arrows representing statistically significant and non-significant (or marginal) relationships respectively. Positive relationships are represented by green arrows, whereas negative relationships are represented by blue arrows. Coefficients are presented on the transformed scaled for care duration (logit) and litter size (log)



**FIGURE 3** Predictions (with 95% confidence intervals) from the parametric models linking the probability to continue maternal care from 1.5 to 2.5 years to its determinants in (a) both Swedish brown bear populations, and in (b) the North and (c, d) South populations, separately. The parametric model was derived from the best of the causal structures tested for each set of observations (i.e. both populations, North and South). Observations are also shown on graphs as means  $\pm$  standard errors (a and c) or as average yearling mass within a litter as random intercepts in models. Predictions from the South population are also presented, although the effect of yearling mass and litter size were only marginal (yearling mass: *p*-value = 0.051; litter size: *p*-value = 0.053) in this population

## 4 | DISCUSSION

Our objective was to identify the direct and indirect determinants of the duration of maternal care, using the Scandinavian brown bear as a model species. We found that, for brown bears throughout Sweden, the duration of maternal care was directly caused by litter size, but not by yearling mass. However, the causal determinants of the duration of maternal care differed between the two populations studied. Our results suggest that environmental context plays an important role in shaping maternal care tactics and explaining the large variation in the duration of maternal care observed across and within species.

Decisions about parental effort should be driven by the optimal balance between their associated costs and benefits (Williams, 1966). Maternal care should thus be extended if it improves maternal and offspring fitness. In mammals, extended maternal care is expected when offspring are small or have a reduced growth rate (Lee et al., 1991). Yet, for both Swedish brown bear populations combined, yearling mass had no effect on the duration of maternal care. Instead, litter size directly affected the duration of maternal care, independently of yearling mass. Because the reproductive value of a litter increases with its size, the fitness returns of a greater parental effort when raising larger litters may outweigh the cost of reduced future reproductive success (Winkler, 1987). Parent-offspring conflicts (Trivers, 1974) are also expected to be more pronounced in larger litters (Morris, 1986), which may force females into continued maternal care.

Whereas combining data from different populations increases sample size and our ability to detect the causes of variation in the duration of maternal care in general, it may conceal the importance of local factors. Reproductive rates and duration of maternal care can differ between populations of the same species with different access to resources and different environmental conditions (Borries et al., 2001; Lee, 1996; Lee et al., 1991; Nawaz et al., 2008). Our study shows that, in addition to inter-population differences in its average value, the duration of maternal care can also have different causal determinants between populations, suggesting that environmental context matters. Yearling mass was the central determinant of the duration of maternal care in the North, with lighter yearlings receiving longer maternal care. Maternal mass was also important and litter size had a marginal effect, but only indirectly through their effects on yearling mass; yearlings of lighter females and in larger litters received extended maternal care, because they were smaller. This result supports previous theoretical and empirical studies placing offspring mass as the central determinant of the duration of maternal care (Bowen et al., 2001; Dahle & Swenson, 2003a; König & Markl, 1987; Lee et al., 1991). In the South, however, apart from the trends detected for litter size and yearling mass, none of the offspring or maternal-related characteristics affected the duration of maternal care when controlling for temporal variation. This difference may stem from the different environmental context experienced by brown bears in the two populations. In the North, climate harshness and lower food availability, suggested by overall smaller mass and slower growth rate of females (Zedrosser et al., 2006), may constrain females' energy allocation to reproduction. As a result, the cost-benefit ratio of extending maternal care may be higher, favouring

terminating maternal care as soon as the yearlings are above a certain threshold mass (Dahle & Swenson, 2003a), which corresponds here to ~15 kg. In fact, extended maternal care in the North seems to compensate for reduced cub growth in yearling brown bears, as mass of 2-year-olds was similar, regardless of the duration of maternal care they had received (Dahle & Swenson, 2003a). The more favourable environmental conditions in the South may reduce the costs of longer maternal care and may explain why some females there continue maternal care, regardless of yearling mass. Detecting costs of reproduction in the wild can be challenging (Hamel et al., 2010), potentially because life-history trade-offs are only apparent under limited resources (Stearns, 1989) and can be masked by individual heterogeneity in resources acquisition and allocation (van Noordwijk & de Jong, 1986).

Apart from offspring mass, extension of maternal care may be driven by the prospects of survival gains for offspring (Balme et al., 2017; Lee et al., 1991). In southern Sweden, mortality of brown bear yearlings is mostly due to hunting and intraspecific killing (Bischof et al., 2009), and, thus, likely not related to their mass, although females appear more vulnerable to intraspecific killing (Swenson et al., 2001). By prolonging the period of maternal care, females can provide protection to yearlings from both conspecifics and hunters (Van de Walle et al., 2018). Furthermore, legal hunting pressure is high in the South, which, combined with the legal protection of family groups, provides a survival advantage to females and their cubs when maternal care is extended (Van de Walle et al., 2018). This particularity of the South (in the North, hunting is mostly illegal or management related and thus not restricted to non-members of family groups, Rauset et al., 2016; Swenson et al., 2017) may alter the cost-benefit balance of durations of maternal care there. This artificial survival gain through longer maternal care could explain why, in parallel with the increasing hunting pressure, the duration of maternal care has increased over the last ~30 years in the South (Van de Walle et al., 2018). It is also in line with the growing evidence of human activities, for example, over-exploitation, as the most important agent of trait change in wild populations (Darimont et al., 2009; Law, 2000; Leclerc et al., 2017), with hunting-induced changes in life-history traits, through its regulation or selectivity, being well-documented in game hunting species (Festa-Bianchet, 2003; Mysterud, 2011).

The duration of maternal care can also be adjusted so offspring become independent under more favourable conditions (Balme et al., 2017; Gruebler & Naef-Daenzer, 2008). Yearling and maternal mass have recently declined in the South population (Leclerc et al., 2016), suggesting that longer maternal care observed today might be caused by increases in population density during the study period (Bischof et al., 2018; Swenson et al., 2017). However, we did control for temporal changes in our analyses and the duration of maternal care was not affected by maternal nor yearling mass, that is, traits on which density dependence should act (Bonenfant et al., 2009). Nevertheless, based on a post hoc analysis using an index of local density, we found a direct link between density and maternal mass, but not between density and yearling mass or between density and the duration of maternal care (Supporting Information S4). Therefore, at higher local density, females are smaller, which results in smaller yearlings, but this does not seem to affect whether a female will continue maternal care



or not. Another alternative explanation could be that females extend maternal care to match with periods of high food abundance (Balme et al., 2017; Gruebler & Naef-Daenzer, 2008). In the South, bilberry *Vaccinium myrtillus* is the most important food source for brown bears in the fall (Stenset et al., 2016). Based on a restricted dataset (10 years) comprising years when an index of annual bilberry production was estimated (Hertel et al., 2018), we found that food availability directly affected both maternal and yearling mass (Supporting Information S5). However, none of these variables were linked directly or indirectly to the duration of maternal care.

In many mammalian species, such as most pinnipeds and many ungulates, maternal care ceases after nutritional independence. For those species, offspring condition at weaning is a crucial determinant of post-weaning survival (e.g. Bowen et al., 2001; Festa-Bianchet et al., 1997). In social mammals, however, offspring can remain within the social group well-beyond nutritional independence, and still receive maternal care through diverse forms, such as comfort in chimpanzees, *Pan troglodytes* (Bădescu et al., 2017), teaching and social assistance in spotted hyenas *Crocuta crocuta* (Hofer & East, 2003), which may lead to delayed survival or reproductive benefits for offspring that are independent of their condition. Despite our ignorance of the relative importance of milk in brown bear cub's diet as they age, we know that yearlings can well-survive on their own and thus may be nutritionally independent at this stage. During the second year of maternal care, we thus expect other forms of care to be provided to brown bear cubs. Brown bears are considered as non-social, however they do form matrilineal lines (Støen et al., 2005). The extension of maternal care in this species could thus serve an additional, yet still unexplored, social and/or teaching purpose and evaluating its benefits should thus also account for those potentially delayed benefits for offspring.

Finally, all of the above assumes that the termination of maternal care results from a female-based decision. A previous study in the South showed that the duration of maternal care may be constrained by sexual conflicts (Van de Walle et al., 2019), with males playing an important role in the termination of maternal care (Dahle & Swenson, 2003b), which has been reported in carnivores and primates (Elliot et al., 2014; Morino & Borries, 2017). Limitations in sample size, however, prevented us from accounting for male-female interactions in our path analyses, but we acknowledge that factors independent of a female's decision, such as sexual conflicts, may explain the duration of maternal care.

In species with large variations in the duration of maternal care (e.g. 1 year in our study), the need to understand and identify the drivers of the duration of maternal care and its demographic consequences is obvious. However, small variations in this trait also can have measurable consequences for offspring fitness (Bowen et al., 2001). The termination of maternal care can also determine the timing of female availability for the next conception, which, in turn, may affect mate choice and have a downstream rippling effect over the events following in the reproductive cycle (Hogg et al., 2017). Observing family break-up and documenting the end of maternal care in the wild is challenging, especially in species with large home

ranges. However, data from long-term and individual-based studies on a large number of individuals are increasingly becoming available. Combined with the evaluation of context-specific costs and benefits associated with different maternal care tactics, this should help further disentangling the determinants of the duration of maternal care in wild animal populations.

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## AUTHORS' CONTRIBUTIONS

J.V.d.W., F.P. and A.Z. conceived and designed the study; A.Z. and J.E.S. coordinated the project and data collection; J.V.d.W. analysed the data and wrote the first draft. All the authors contributed to the interpretation of the data and subsequent manuscript writing and revisions.

## DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.fttdz08r1> (Van de Walle et al., 2020).

## ORCID

Joanie Van de Walle  <https://orcid.org/0000-0002-5137-1851>

Jon E. Swenson  <https://orcid.org/0000-0002-5463-4282>

Fanie Pelletier  <https://orcid.org/0000-0002-0113-5412>

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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