

The role of maternal behavior and offspring development in the survival of mountain goat kids

Rachel Théoret-Gosselin · Sandra Hamel ·
Steeve D. Côté

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Abstract Studies on juvenile survival have mainly focused on the effects of environmental conditions and maternal traits. However, growing evidence indicates that the ability of parents to care for their young and the offspring developmental behaviors could be key determinants of their survival. We examined the relative influence of (1) environmental conditions, (2) offspring traits, (3) maternal traits, (4) maternal care behaviors, and (5) offspring developmental behaviors on kid survival to weaning and to 1 year old in mountain goats (*Oreamnos americanus*). Offspring development and maternal care directly affected offspring survival, and this more importantly than did environmental conditions and maternal traits. Frequency of play strongly increased survival before weaning. Greater maternal care increased offspring survival during winter, directly and indirectly through kid mass. Kid mass was also a major determinant of both summer and winter survival. Environmental conditions mainly influenced summer survival while maternal characteristics indirectly affected winter survival through an effect on kid mass. Behavioral adaptations of maternal care and offspring development to

local selective pressures can lead to local adaptations and have greater implications in population dynamic studies than previously believed.

Keywords Maternal care · Maternal effect · Offspring survival · Path analysis · Suckling

Introduction

Most life-history studies assessing the determinants of offspring survival have focused on the influence of environmental conditions, maternal traits, and offspring characteristics (Gaillard et al. 1998). Although parental care and offspring development are likely key determinants of offspring survival (Bernardo 1996; Therrien et al. 2008; Mousseau et al. 2009), their influence is often neglected when evaluating offspring survival in mammals. Indeed, maternal traits like age and condition and offspring characteristics such as mass are used as proxies for maternal care. However, the relationships between maternal traits, offspring condition and offspring survival are likely to be indirect and probably result from maternal care and offspring developmental behaviors (Andersen et al. 2000). Therefore, it is essential to test both maternal traits and care, and both offspring traits and development, as well as environmental factors, against offspring survival to disentangle the direct and indirect determinants of juvenile survival, a fundamental component of population dynamics (Gaillard et al. 1998).

In most polygynous mammals, parental care is given strictly by females. Lactation is the most important caring behavior providing the main source of energy for offspring early in the development (Oftedal 1985). Nursing behaviors are therefore likely to directly influence offspring growth,

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R. Théoret-Gosselin · S. D. Côté
Département de biologie and Centre d'études nordiques,
Université Laval, Québec, QC G1V 0A6, Canada

S. Hamel (✉)
Department of Arctic and Marine Biology, Faculty
of Biosciences, Fisheries and Economics, University of Tromsø,
9037 Tromsø, Norway
e-mail: sandra.hamel@uit.no

and thereby indirectly affect offspring survival because mass is an important determinant of offspring survival (Gaillard et al. 1997; Loison et al. 1999). In addition, maternal efforts to maintain proximity with her young can directly enhance offspring survival by reducing predation risk (Grovenburg et al. 2012). Maternal efforts to maintain proximity and to provide an adequate social environment will also strengthen the mother–young bond, thereby providing juveniles with the abilities to cope with stressful situations (Nowak et al. 2000; Spinka et al. 2001; Fagen and Fagen 2004). Offspring social and locomotor development through play behavior should improve motor skills and locomotor versatility, as well as emotional resilience to unpredictable events, thereby providing offspring with abilities to escape predators (Spinka et al. 2001; Nunes et al. 2004).

Maternal traits can directly affect offspring mass and thereby indirectly influence survival (Bernardo 1996; Solberg et al. 2007). Females in poor nutritional condition and with low body fat reserves generally give birth to light young and are potentially unable to satisfy their progeny's nutritional needs because they produce less or low quality milk (Landete-Castillejos et al. 2009). Offspring cared by older females may have higher survival because older mothers are likely to provide greater allocation than younger mothers due to their increased reproductive experience or reduced reproductive value (Pianka and Parker 1975; Solberg et al. 2007; Meijer et al. 2011). Other maternal traits, such as social rank or home range quality, can also indirectly enhance juvenile survival through access to high quality forage and reduced vulnerability to predation (Clutton-Brock et al. 1984; Van Moorter et al. 2009). Because offspring depend mostly on maternal care before weaning (Nowak et al. 2000), maternal traits could also indirectly affect juvenile survival through their influence on maternal care itself.

Several studies have revealed the influence of environmental conditions on juvenile survival. In large herbivores, environmental conditions associated with access to high quality forage, such as an early green-up of vegetation in temperate ecosystems, high habitat productivity, or low population density, can enhance juvenile growth and thereby indirectly affect survival (Coulson et al. 2001; Hamel et al. 2010). Other environmental factors, like predation risk or snow depth, influence habitat selection and movement patterns, and can therefore affect juvenile growth through impacts on energy expenditure and forage availability (Frid and Dill 2002). In general, favorable environmental conditions increase juvenile survival through an indirect positive influence on offspring traits such as enhanced body growth, fat reserves, or mass. Environmental conditions can also have an indirect impact on offspring survival through their influence on maternal condition (Festa-Bianchet and Jorgenson 1998).

In this study, we assessed the summer and winter survival probabilities of mountain goat (*Oreamnos americanus*) kids using 15 years of longitudinal data from marked individuals. Our objectives were to determine the relative influence of (1) environmental conditions, (2) offspring traits, (3) offspring developmental behaviors, (4) maternal traits, and (5) maternal care behaviors on kid survival to weaning (summer survival) and to 1 year old (winter survival). Using the most influential factors revealed in a first set of regression analyses, we further examined with path analyses the causal patterns, i.e., direct or indirect effects, of these variables and how they interacted among each other to influence kid survival. We expected environmental conditions and maternal traits to affect kid survival, but only indirectly through their influence on kid mass. We hypothesized that greater maternal care would enhance summer and winter survival, both indirectly, through increased energy allocation enhancing offspring mass, and directly, through the strength of the maternal–neonate bond. We expected heavy, old, and dominant females to provide greater maternal care than light, young, and subordinate mothers. In addition, we expected offspring locomotor development to influence survival positively over winter because of improved muscular development and capacity to cope with stressful situations (Spinka et al. 2001).

Materials and methods

Study area and captures

We studied mountain goats at Caw Ridge (54°N, 119°W), west central Alberta, Canada. Goats used an area of approximately 28 km² of alpine tundra and open subalpine forest of Engelmann spruce (*Picea engelmannii*) at 1,750–2,170 m in altitude. The climate is subarctic-arctic, characterized by short, cool summers followed by long, harsh winters. The main predators of mountain goats in the study area are wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), and cougars (*Puma concolor*). Black bears (*U. americanus*), coyotes (*C. latrans*), wolverines (*Gulo gulo*), and golden eagles (*Aquila chrysaetos*) may also predate on mountain goats (Festa-Bianchet and Côté 2008).

We used longitudinal data from marked females with a kid at heel from 1995 to 2010. Since 1988, we have captured goats using remotely-controlled box traps and self-tripping Clover traps baited with salt, and marked them with colored ear tags and visual collars. Since 1993, 98 % of goats aged 1 year or older have been marked. For females not marked as yearlings, we determined their age by counting the number of horn annuli, a method reliable up to 7 years of age (Stevens and Houston 1989). Since 1998, we have not captured any adult female with a kid

at heel, or any kid, to avoid kid abandonment (Côté et al. 1998). We excluded data from all mothers and kids captured in earlier years to avoid potential bias.

Survival

From mid-May to mid-September, we observed goats almost daily with spotting scopes ($\times 15$ – 45). Identity (ID) of mothers was determined from observation of nursing behaviors and later confirmed using genetic analyses. We determined kid sex by the urination posture and the observation of the black vulvar patch for females (Côté and Festa-Bianchet 2001b). No kid was ever missing for more than 1 week and subsequently re-sighted, thus we considered kids that disappeared for 7 days as dead. Kid-ding period was highly synchronized and occurred mainly between 20 May and 3 June (Côté and Festa-Bianchet 2001b). We defined kid summer survival as survival from birth until weaning, i.e., 15 September (Côté and Festa-Bianchet 2001b), and winter survival as survival from weaning until 1 June the following year. We determined the identity of kids that survived over the winter from observations of close associations with their mothers in the spring and from DNA analyses of skin samples collected during marking.

Environmental conditions

To characterize winter conditions, we used the November–March anomalies of the North Pacific Index (NPI; Trenberth and Hurrell 1994). For our study site, high values of NPI represent snowy and cold winters and low values correspond to less snowy and mild winters (Hamel et al. 2009a). We used two indices: one representing winter conditions during the pre-natal period (NPI gestation) and the other describing winter conditions during the first winter of the kid (NPI winter). To characterize annual variation in vegetation availability in the spring, we used the sum of the bimonthly Normalized Difference Vegetation Index (NDVI; Pettorelli et al. 2005) of June. At Caw Ridge, high NDVI values correspond to rapid spring green-up, representing early access to vegetation (Hamel et al. 2009b). We used the total number of goats in the population on 1 June as a measure of population density.

Masses

We recorded masses (± 0.5 kg) with three remotely-controlled electronic platform scales placed at the trap site and baited with salt. We could therefore weigh many individuals, especially kids, without handling them. Because we recorded several masses throughout the summer for the same individual, we adjusted mother masses to 15 July

using the average daily summer mass gain for five age classes of females (3, 4, 5, 6 and ≥ 7 years old; see Hamel et al. 2010). Because mass increased with age until approximately 7 years of age (Côté and Festa-Bianchet 2001a) and senescence does not occur in female mountain goats (see Electronic Supplementary Material, ESM1), we calculated age-specific masses as the residuals of the cubic regression of mass on age using age as a continuous variable from 3 to 7, where age 7 included all females 7 years and older. The predictions we obtained for ages 3 to 7 using the cubic regression were similar to the predictions we obtained fitting a spline for ages 3 to 14. We also adjusted kid masses to 15 July using the average summer mass gain for each sex (males 217.0 ± 9.3 g/day; females 202.9 ± 8.4 g/day), which were obtained from a linear mixed model with mother ID as a random intercept. Further description of capture and marking techniques can be found in Côté et al. (1998).

Behavioral observations

From 1995 to 2010, we recorded 483 focal observations on 267 mother-kid pairs (from 1 to 6 observations per pair; Altmann 1974). From the observed dyads, 209 kids survived to weaning (summer survival = 78 %, ranging from 55 to 100 % each year) and 162 survived from weaning to 1 year old (winter survival = 78 %, ranging from 50 to 100 %). We followed each dyad for a minimum of 30 subsequent minutes to a maximum of 120 min, for a total of 756 h of observations. Every 2 min, we recorded the estimated distance between the dyad members and their respective direction of movement according to the other's position: approaching (moving towards the other), leaving (moving away), or neutral (Hinde and Atkinson 1970). During the entire focal observation, we recorded the identity of any individual observed within 4 m of the kid (considered as an opportunity for interaction; Côté 2000) and noted when an aggressive interaction towards the kid occurred. Every time the kid's muzzle touched its mother's udder, we recorded the duration of the contact in seconds with stopwatches (± 1 s). These behavioral observations were used to define eight variables for characterizing maternal care and kid development processes (Table 1). We log-transformed these variables because they all followed a Poisson distribution. We used frequency of locomotor play, frequency of play behavior, and frequency of social interaction to evaluate offspring physical and social development (Table 2).

To define maternal allocation and quality of maternal care, we computed an index that combined a mother's nursing efforts with her efforts to maintain proximity to her kid (hereafter called maternal care; Table 2). Although suckling duration and frequency have been shown in some species

Table 1 Description of the behavioral variables representing (a) kid developmental processes and (b) maternal care for mountain goats (*Oreamnos americanus*) at Caw Ridge, Alberta, Canada (1995–2010)

Variables	Description	References
(a) Kid development		
Frequency of locomotor play	Number of locomotor behavior per hour. Mountain goat kids mainly exhibit frolic behavior (jumping with exuberant head tosses and random kickings)	(McDonnell and Poulin 2002)
Frequency of play	Number of social playing behavior (with other kids or its mother) divided by the number of interaction possibilities with kids or mother (per hour)	(Côté 2000)
Frequency of interactions	Number of interactions performed by adults towards the kid divided by the number of interaction possibilities (per hour)	(Côté 2000)
(b) Maternal care		
Dyad distance	Median distance between the mother and the kid while the kid is active	(Green 1992)
Contact-maintenance index	The percentage of “leaving” movements initiated by the kid (out of the total “leaving” movements initiated in the dyad) minus the percentage of “approaching” movements initiated by the kid (out of the total “approaching” movements initiated in the dyad)	(Green 1992; Hinde and Atkinson 1970)
Frequency of suckling	Number of suckling events per hour	
Total suckling duration	Mean suckling duration in seconds multiplied by the frequency of suckling ($s h^{-1}$)	(Therrien et al. 2008)
Frequency of suckling rejection	Number of suckling rejection events per hour	(Therrien et al. 2008)

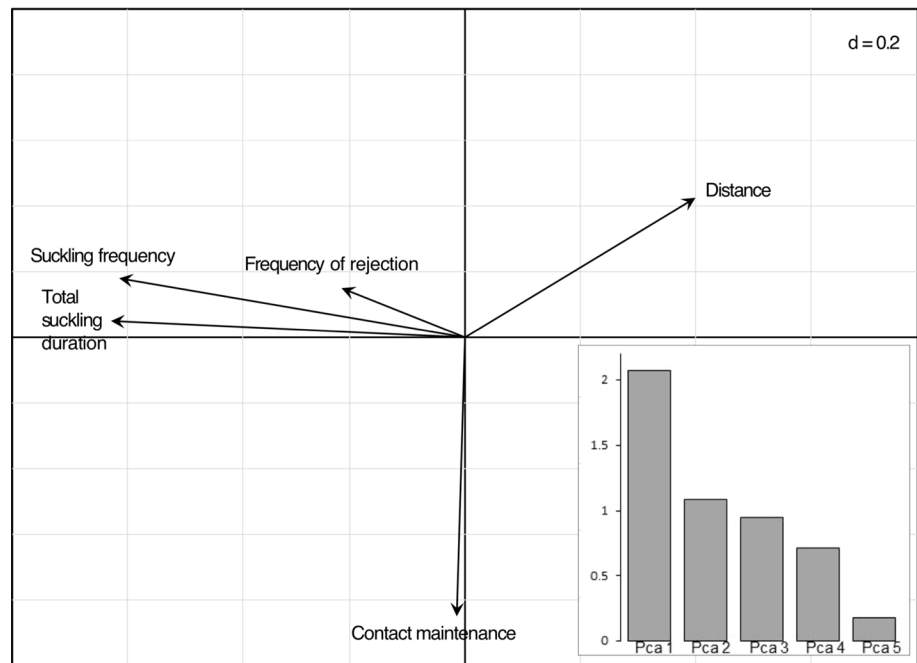
Table 2 Summary of the variables included in the analyses of kid survival for mountain goats at Caw Ridge, Alberta, Canada (1995–2010)

Category	Variables included
Environmental conditions	Population density NDVI NPI gestation NPI winter
Offspring traits	Kid mass Sex
Offspring development	Frequency of locomotor play Frequency of play Frequency of interactions
Maternal traits	Age-specific mass Age-specific social rank Age
Maternal care index	Dyad distance Contact-maintenance index Frequency of suckling Total suckling duration Frequency of suckling rejection

to adequately reflect milk intake and to correlate positively with offspring mass, this relationship does not hold for all species (Cameron 1998). In these cases where a negative relationship was found, suckling duration and frequency were presumed to be a behavioral indication that milk transfer was insufficient, with longer and more frequent suckling likely representing offspring dissatisfaction, and thereby mother–offspring conflict. It was thus suggested to account

for the frequency of suckling rejection when measuring suckling duration and frequency, and importantly, to avoid describing maternal care by a single behavioral variable. We therefore performed a principal component analysis (PCA) that included suckling duration and frequency, along with the frequency of rejected suckling and two spatial variables, the dyad distance and the contact-maintenance index (Tables 1, 2). We thereby obtained a maternal care index that accounted for many behavioral measures. The first axis of the PCA explained 41 % of the variance and was the only influential axis (as determined by the rapid decrease in consecutive eigenvalues; Cattel 1966; Fig. 1). We therefore used the scores of the first axis as an index of maternal care. Positive scores represented kids that nursed less frequently, for a shorter total duration, with suckling attempts that were seldom rejected, and that stayed more distant to their mother (Fig. 1). The contact-maintenance index was not an influential variable (Fig. 1). As suckling duration and frequency were positively correlated with suckling rejection (Fig. 1), suckling duration and frequency likely represented inefficient milk transfer. These variables were negatively related to distance to the mother, suggesting that kids that were nursed less efficiently attempted to suckle more frequently and thereby remained in closer proximity as they were more often soliciting their mother because their needs were not satisfied. Therefore, positive scores overall represented greater maternal care, as confirmed by the positive influence of this index on kid mass (see “Results”). The scores were positively correlated with summer day ($r = 0.63$). To control for variation in maternal care over the summer, we adjusted these scores to 15 July using a regression equation [intercept (\pm SE) = -6.54 ± 0.37 , slope = 1.63 ± 0.09]

Fig. 1 Results of the principal component analysis (PCA) of maternal care index for mountain goats (*Oreamnos americanus*) at Caw Ridge, Alberta, Canada (1995–2010). Correlations among care variables are indicated by the arrows for which the length gives the value of the correlation. Correlations can be measured using grid lines (separated by 0.2). Bar plot on the right lower corner shows eigenvalues of the PCA



obtained from a linear model where the date was log-transformed. For dyads with more than one observation, we used the mean of the scores.

We determined the social rank of each mother annually based on ad libitum observations of agonistic interactions recorded among adult females over summer. Because relationships were highly linear every year, we applied the method of de Vries (1998) using Matman 1.0 for Windows (Noldus Information Technology 1998) to order adult females in an annual hierarchy (see Côté 2000 for details). Social rank was strongly related with age each year. Because the relationship between age and social rank was not always linear, we determined each year the best polynomial regression that was necessary to fit the relationship (polynomial of degrees 1, 2 or 3). We then used the residuals of the best polynomial regression of rank on age to obtain age-specific social ranks for each year.

Statistical analyses

To assess the direct and indirect relationships among the variables measured, we used path analysis to compare different causal models. A causal model is not likely to be valid if it includes too many variables not influencing the final variable (here survival; Shipley 2002). Therefore, because we had numerous variables and it was possible that some of them would have no effect, we carried the statistical analyses in two steps. First, as an exploratory step, we evaluated which of all the explanatory variables influenced kid survival over the summer and over the winter using generalized linear mixed models (GLMMs). This step was

therefore performed to select the variables having an influence on survival. In a second step, we used path analyses to assess the structural relationships among the predictors selected in the first step. We standardized all continuous variables to allow the comparison of the relative influence of each predictor with one another (Schielzeth 2010). Because our models included a binary predictor (kid sex), we standardized the variables by dividing the continuous variables by two standard deviations (Gelman 2008). We also centered independent variables to remove the collinearity between the main effects and the interactions, therefore allowing us to correctly execute model averaging (see below; Schielzeth 2010). We also tested for multicollinearity and found no strong correlation among the variables (all r values < 0.4). Furthermore, because our dataset included some missing data (12 % missing at random) in several explanatory variables, we used multiple imputations to avoid biases in the model selection process (Nakagawa and Freckleton 2008, 2011). The procedure uses bootstrapping to provide data points for every missing data (Schafer 1999; Nakagawa and Freckleton 2011). We used the R function “amelia” (Honaker et al. 2011; R Development Core Team 2011) to produce 10 imputed datasets (as recommended by Rubin 1987). We performed all subsequent analyses included in the two analytical steps on the ten imputed datasets.

First step: variables selection

We used GLMMs (“glmer” function from the R package “lme4”, with a logit link and mother ID as a random

intercept; Bates et al. 2012) to assess the effect of (1) environmental conditions (population density, NDVI, NPI gestation, and NPI winter), (2) offspring traits (mass and sex), (3) offspring development (frequency of locomotor play, frequency of play behavior, and frequency of interaction), (4) maternal traits (age-specific mass, age-specific social rank, and age), (5) maternal care, and (6) relevant interactions on kid survival over the summer and over the winter (see Table 2 and ESM2). The dataset for summer survival ($n = 267$ kids from 99 mothers) was slightly larger than for winter survival ($n = 209$ kids from 90 mothers) because the latter excluded kids that died over the summer. We determined whether a variable was an influential predictor of offspring survival using a model selection approach based on the Akaike's information criterion adapted for small samples (AICc; Burnham and Anderson 2002). We identified a list of models a priori for each dependent variable (43 models for summer survival and 41 for winter survival; see ESM2), and computed for each model the average Δ AICc obtained from the ten imputed datasets analyzed. We considered all models with a mean Δ AICc of 4 or less (sensu Burnham et al. 2011) as providing plausible support to the data (9 models for summer survival and 22 for winter survival; see ESM2). We used model averaging among models with plausible support rather than selecting the most-supported model because our goal in this exploration step was not to determine the most influential variables but rather to select all the variables having an effect on survival. Therefore, we performed model averaging among plausible models and determined whether each variable included in the plausible models had an effect by examining its estimate and effect size, i.e., adjusted estimates and their 95 % Bayesian credible intervals (CIs). These were obtained from Markov chain Monte Carlo (MCMC; 10,000 iterations) bootstraps set on posterior distribution of the parameters (see Baayen et al. 2008 for details). For linear mixed models, adjusted estimates and CIs can be obtained using the function "pvals.fnc" in the "languageR" package (Baayen et al. 2008). Since this function is not yet implemented for GLMMs, we used a R script (see Hamel et al. 2012) based on similar methods as the function "pvals.fnc" that can calculate adjusted estimates and CIs for GLMMs (Baayen et al. 2008). Because we had ten imputed datasets, we had ten estimates for each variable included in a model. We therefore averaged the estimates using the corresponding AICc weight for each model in a given dataset. We calculated the median of the averaged estimates and the corresponding lower and upper boundaries of the CIs for all the variables included in the selected models. Finally, to determine the importance of each predictor, we computed the percentage of time the CI of a variable excluded zero out of all the estimates obtained for that variable (see Table ESM3.1 in ESM3).

Second step: confirmatory multilevel path analysis

Once we had determined the influential predictors, we assessed structural relationships among them using generalized multilevel path models following Shipley's method of directional separation tests (d-sep tests; Shipley 2000, 2002; see also ESM4). The results of the first selection of variables included several variables with a weak effect on survival (see Table ESM3.1). This probably resulted from the multiple imputation process, as there is a greater chance of finding a statistically significant result in one of the ten imputed datasets just by chance because of the repetition of the analysis. Therefore, to avoid over-parameterization in the path models, we only used variables and interactions with CI excluding zero for more than 10 % of the models, i.e., corresponding to the inclusion of variables that were having an effect in more than one imputed datasets. Nevertheless, we included "population density" in the path models for summer survival even if it had only 4 % of CIs excluding zero, because an interaction including this variable was included (Table ESM3.1a). For the same reason, we included "maternal mass" and "maternal social rank" in the path models describing winter survival (0 and 5 % of CIs excluding zero, respectively, Table ESM3.1b). Based on our knowledge of the population dynamics of goats at Caw Ridge (Côté and Festa-Bianchet 2001a, b; Festa-Bianchet and Côté 2008) and on the results obtained in our first analytical step, we constructed nine causal models (called directed acyclic graphs, DAGs; see Shipley 2002) to describe the hypothesized relationships among the variables influencing summer survival (hypotheses S1–S9) and 19 for winter survival (hypotheses W1–W19). We only present the best DAG model (lowest C value with high p value of the goodness-of-fit test indicates that the model provides a strong fit to the data; Shipley 2002) for each survival, but all DAGs tested are presented in ESM4. Once the best causal model was found, we calculated the strength of each path as the coefficients estimated from the mixed models derived from the DAGs (Shipley 2009). As described above, we obtained adjusted estimates and CIs for each path with MCMC bootstrapping methods. Because we obtained ten estimates (i.e., from the ten imputed datasets), we presented the median estimate and its corresponding CI. The selected causal models for summer and winter survival included a few variables with unclear relationships (path coefficients with 95 % credible intervals including zero), but we kept these relationships because these models provided the best fit to the data (B. Shipley, personal communication). To determine the global effect of each predictor on survival, we calculated the estimates provided from simple GLMMs between each variable and survival (Shipley 2002).

Results

Selection of variables

NPI during gestation, kid mass, kid sex, maternal mass, the interaction between maternal mass and density, and the frequency of locomotor play were the variables that influenced summer survival (Table ESM3.1a). Winter survival was affected by NPI during gestation, NPI during the first winter, density, kid mass, the interaction between maternal mass and maternal social rank, maternal care, and the frequency of play behaviors (Table ESM3.1b).

Path analysis for summer survival

NPI during gestation, the interaction between age-specific maternal mass and population density, kid mass, and frequency of locomotor play directly determined offspring summer survival (Fig. 2a; C value = 29.6, $k = 15$, $p = 0.5$). The strongest effect on survival was the positive direct effect of frequency of locomotor play: the survival probability was seven times more likely for each increase of one unit of locomotor play (on the log scale; Figs. 2a, 3a). Kid mass and NPI during gestation were two other important direct determinants: a kid was three times more likely to survive to weaning for each increase of 1 kg, but it was two times less likely to survive if the NPI during gestation was high, i.e., snowier and colder winter (Fig. 2a). The interaction between population density and maternal mass had a direct negative influence on survival, but this effect was weak (CI widely included zero). Age-specific maternal mass, the interaction between age-specific maternal mass and population density, and kid sex had an indirect effect on summer survival through their effects on kid mass. Age-specific maternal mass was the strongest determinant of kid mass (Figs. 2a, 3c), while the influence of the other two variables was weak as their CI included zero (Fig. 2a). Finally, kid mass had a slight negative influence on the frequency of locomotor play, slightly diminishing the overall effect of kid mass on survival to weaning [global odds ratio (OR) = 2.0 (1.1, 3.9), see ESM5 for how to interpret OR].

Path analysis for winter survival

NPI during gestation and during the first winter of the kid, maternal care, kid mass, and frequency of play had direct effects on winter survival (Fig. 2b; C value = 54.1, $k = 27$, $p = 0.5$). Even though the global effect of kid mass was slightly lowered by the negative indirect effect it had through the frequency of play, it remained the primary determinant of winter survival. A kid was almost three times more likely to survive its first winter for each increase of 1 kg [global OR = 2.6 (1.3, 5.4); Fig. 2b]. A

kid was two times more likely to survive the winter if its mother presented a high care index, i.e., giving short and infrequent suckles, but rarely rejecting suckles, and having a greater kid-mother distance [global OR = 2.5 (1.1, 5.0); Figs. 2b, 3b]. The influence of the frequency of play behavior on winter survival was highly variable and imprecisely estimated (large CI), but overall kids with a higher frequency of play had a higher survival than kids with a lower frequency of play (Fig. 2b). The effects of environmental conditions during gestation and during the first winter on winter survival were weak [global OR during gestation = 0.6 (0.3, 1.3) and global OR for the first winter = 1.4 (0.6, 3.3); Fig. 2b]. Similarly to summer survival, age-specific maternal mass only had an indirect positive effect on winter survival through its positive influence on kid mass, but its global effect on survival was weak [global OR = 1.0 (0.5, 2.1); Fig. 2b]. In addition to its direct effect on survival, maternal care index had an indirect positive influence on kid mass (Fig. 2b): kids were bigger if their mother gave short and infrequent suckles, but rarely rejected their suckling attempts, and had a greater kid-mother distance (Fig. 3d).

Discussion

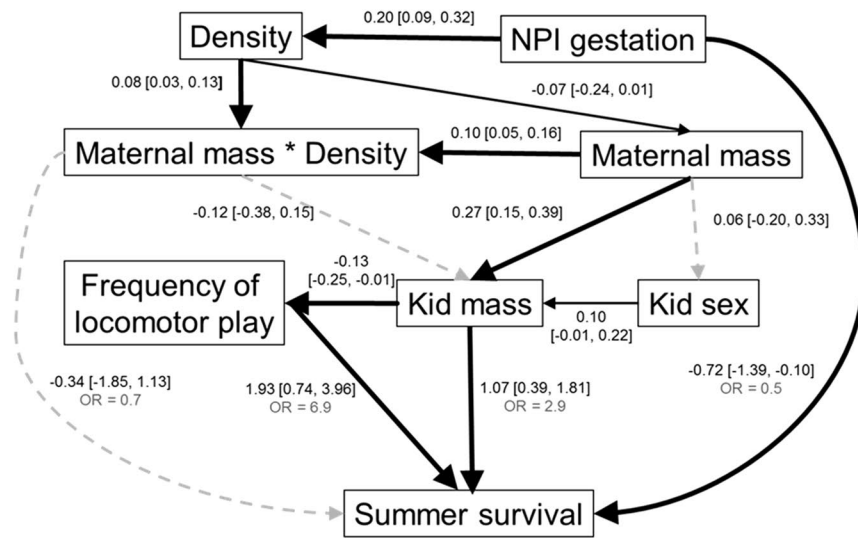
Although offspring development and maternal care are seldom considered as factors influencing juvenile survival in mammals (Nowak et al. 2000; Fagen and Fagen 2004; Cameron et al. 2008), our results show that these behavioral variables are critical and, most importantly, direct determinants of offspring survival. Kid mass is also a major determinant of both summer and winter survival. We confirm the influence of environmental conditions on kid summer survival and the effect of maternal traits on winter survival in mountain goats (Hamel et al. 2010). The originality of our study is that we empirically show that density and maternal traits mainly have an indirect effect on offspring survival through their influence on kid mass. Another novel finding of our research is that, although environmental conditions and maternal traits are frequently evaluated in life-history studies on offspring survival, these indirect determinants have weaker effects on juvenile survival than kid development and maternal care. As environmental conditions only had small effects on kid survival and were not central to our study, the discussion of these effects has been placed in Electronic Supplementary Material (ESM6).

Kid development

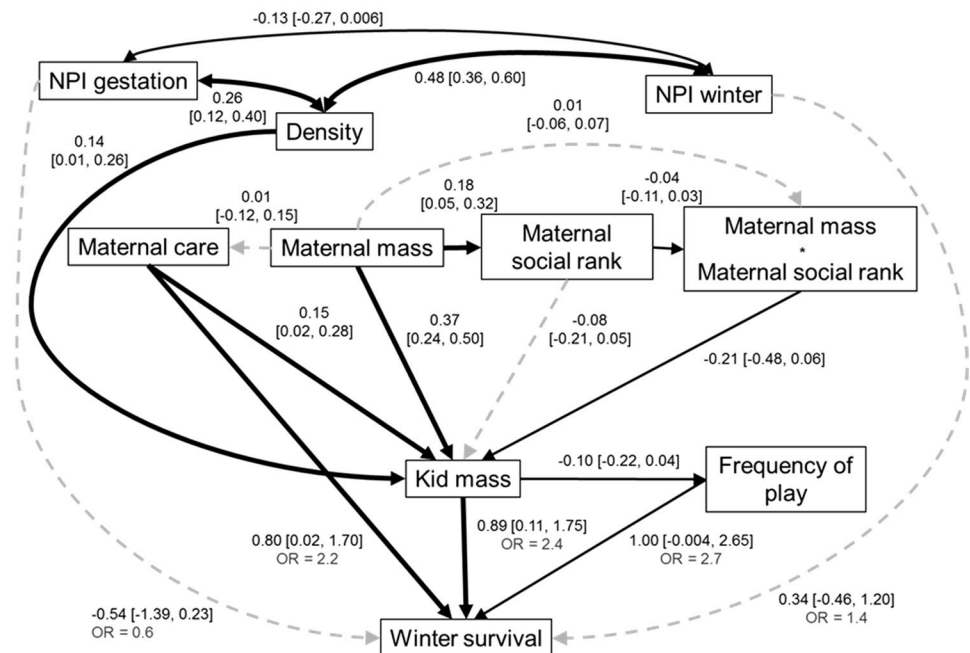
Locomotor development is the strongest predictor of summer survival and is also a determinant of winter survival. Similarly to our results, short-term positive effects of play

Fig. 2 Path analysis models of the direct and indirect influence of environmental conditions, maternal characteristics, and kid's characteristics on **a** summer survival and **b** winter survival of mountain goat kids at Caw Ridge, Alberta, Canada (1995–2010). Standardized partial-regression coefficients with their associated 95 % credible intervals (CI) are presented above each path, where the *arrows* indicate the direction of the causal relationships. *Thick and black solid lines* represent paths with good evidence of an effect (95 % CI not overlapping zero), *thin black solid lines* indicate weak evidence for an effect (95 % CI including marginally zero; <0.05), and *thin gray dotted lines* stand for unclear relationships (95 % CI including zero). *Double-headed lines* represent correlations among independent variables that cannot be explained by causation. Odds ratios (OR) are presented in *gray* for the variables having a direct effect on survival (see ESM5 for how to interpret OR). Mother identity was included as a random effect

(a) DAG representing the probabilities to survive to weaning



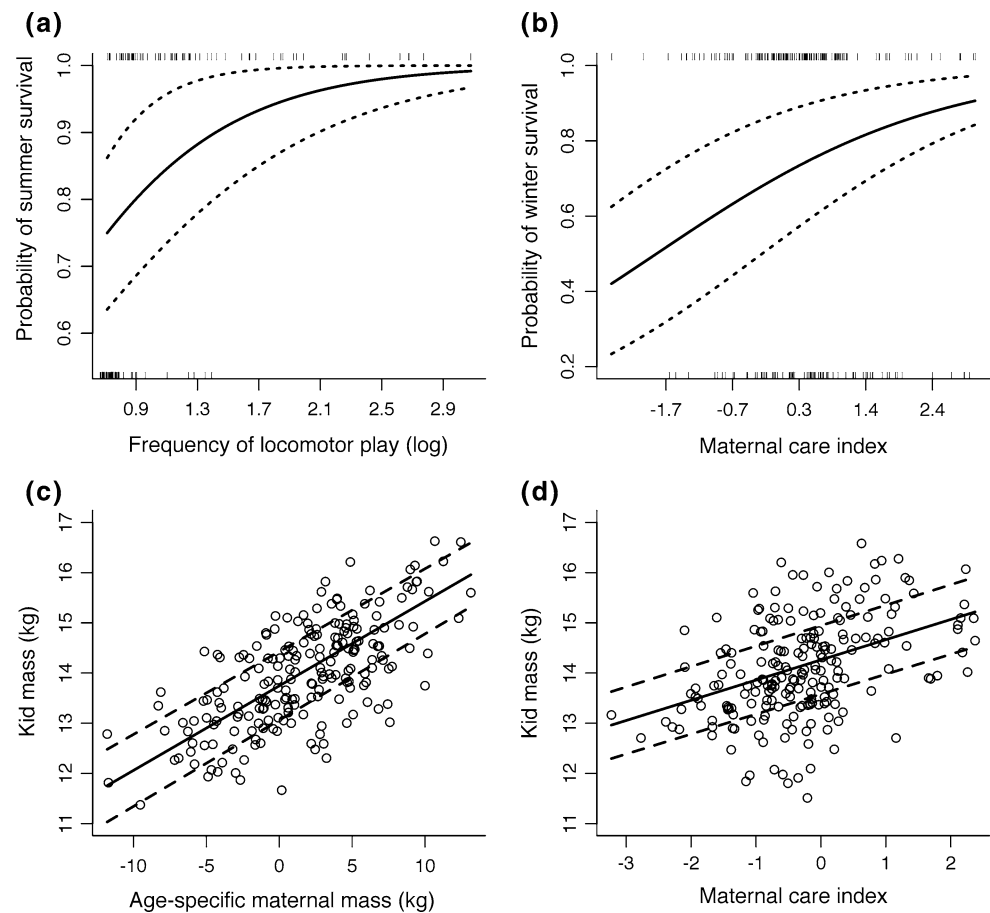
(b) DAG representing the probabilities of winter survival



behavior on juvenile survival are found in grizzly bears (Fagen and Fagen 2004) and in feral horses (*Equus caballus*; Cameron et al. 2008). The latest and most accepted hypothesis on the function of play states that these behaviors develop motor skills, locomotor versatility, and emotional resilience to unpredictable events (Spinka et al. 2001; Nunes et al. 2004). Because the greatest cause of mortality for ungulate neonates during their first summer is predation (Linnell et al. 1995), this hypothesis could explain the strong effect of play behavior on kid summer survival. Agile juveniles showing good coordination in their movements acquired through play

experiences are probably less susceptible to be caught during a predator attack and could show a proper response to the stress of an attack (Spinka et al. 2001). The weaker but also positive effect of play on winter survival could also be related to higher plasticity of movements developed through play behavior. Kids' agility could slightly help them cope with harsh winter conditions when higher muscle endurance and better equilibrium are required for difficult movements in snow. Spinka et al. (2001) proposed that play behaviors could enhance the emotional resilience to stress not only for unpredicted events but also in stressful group situations

Fig. 3 Direct and indirect effects emphasized by the best DAG on survival (*top panels*) and kid mass (*bottom panels*) of mountain goat kids at Caw Ridge Alberta, Canada (1995–2010). Influence of the frequency of locomotor play on kid summer survival (**a**), of maternal care index (length and frequency of suckling bouts, frequency of suckling rejection, and mother–kid distance) on kid winter survival (**b**), of maternal mass (corrected for maternal age) on kid mass (**c**), and of maternal care index on kid mass (**d**). *Continuous lines* represent the predicted values from the mixed models, *dotted lines* are the 95 % credible intervals, and the *vertical lines (top panels)* and *dots (bottom panels)* are the raw data



because play could reduce aggressiveness in gregarious species. As in other aggressive species, agonistic interactions directed towards juveniles can create stressful situations and play behaviors could enable offspring to cope with stress and ultimately be beneficial for early survival (e.g., feral horses; Cameron et al. 2008). Alternatively, the relationship between survival and play behavior could be due to a positive correlation between physical condition and play. For instance, weak individuals could play less frequently, and their lower survival could then be related to body condition instead of play frequency. Our results, however, show the opposite: bigger kids play less frequently than smaller kids. In addition, the relationship between play and kid mass is small and much weaker than the relationship between play and survival, for both summer and winter (Fig. 2). Therefore, although it is not clear why bigger kids tend to play less, there seems to be two potential tactics allowing kids to increase their chances of survival: being bigger or playing more. Experimental testing promoting various level of play behavior (e.g., increasing play opportunities by providing toys or decreasing it by isolating some offspring) could provide information on the mechanisms driving the influence of offspring development on survival and could help unveil why larger offspring play less.

Maternal care

The strong positive effect of the maternal care index on kid mass confirms the concerns on the use of time and frequency of suckling as proxies for the actual quantity of milk transferred to offspring (Cameron 1998). The negative influence of duration and frequency of suckling on both kid mass and kid survival supports that these behavioral observations are not good indicators of the rate of milk intake, but rather reflect that the milk transfer is insufficient (Mendl and Paul 1989; Therrien et al. 2008). Greater maternal care represented by the positive values of our index described a mother–young bond where kids did not need to try harder to fulfill their nutritional needs. Maternal care thus appears to be associated with offspring satisfaction. Our results and the literature (e.g., Therrien et al. 2008) suggest that the frequency of rejected suckling attempts coupled with total duration of suckling and frequency of suckling are good indicators of maternal care.

According to life-history theory, parental care evolved because nutrition and protection provided to offspring improve their survival, and thereby increase the fitness of their parents. Although we hypothesized that maternal care would influence summer survival due to the strong

dependency of young on their mothers, greater maternal care only improves winter survival. Maternal care acted both indirectly and directly on winter survival, which demonstrates the variety of ways that mothers can care for their offspring (Bernardo 1996). An indirect effect through kid mass confirms that maternal milk is a crucial factor in offspring energy intake before weaning (Robbins and Robbins 1979), even if kids start foraging as soon as 5 days old (S.D. Côté, personal observation). The direct effect of maternal care on kid survival further indicates that parental input can go beyond providing food (Bernardo 1996). Although we could not follow goats during winter and causes of death are difficult to identify, predation and starvation in early spring are believed to be the main causes of mortality during the first year of mountain goats (Festa-Bianchet and Côté 2008). Maternal care likely promotes the development of a strong maternal–neonate bond. In ungulates, the maternal–neonate bond is directly related to offspring survival because mothers provide protection against predators (Lingle et al. 2005; Grovenburg et al. 2012), shelter from weather (Blix et al. 1984; Nowak et al. 2000), and knowledge on the survival strategies linked to habitat selection (Moore 2007).

Maternal traits

In addition to maternal care, maternal mass is the only other maternal trait influencing offspring survival. Maternal mass has an indirect effect on both summer and winter survival through its influence on kid mass. Heavy mothers usually give birth to heavy kids, which are larger and have more fat reserves than lighter kids (Taillon et al. 2012), and hence have better chances of survival over their first year (Loison et al. 1999). Because maternal mass directly affects kid mass without passing through maternal care, we conclude that the effect of maternal mass on kid mass is not dependent on milk provisioning and is more likely due to variation in birth mass or prenatal care (Andersen et al. 2000). Maternal body condition, however, could affect care provided by affecting the length of the lactation period or the patterns of allocation, which would not be reflected in the index we used (Babbitt and Packard 1990). Other maternal characteristics such as maternal age have been shown to affect offspring mass and survival in other ungulates (Byers 1997; Hayward et al. 2013), but we found no evidence supporting an age effect in mountain goats. Maternal social rank was negatively associated with kid mass, but the relationship was weak and not statistically significant. Furthermore, the lack of clear relationships between maternal traits and maternal care may suggest that other characteristics may play a role in caring behaviors. For instance, anti-predator behavior (Lingle et al. 2005; Grovenburg et al. 2012), the capacity to find high-quality forage, experience

in providing care (Meijer et al. 2011), or individual temperament (Réale et al. 2007) could be better determinants of maternal care than maternal body condition.

Our study demonstrates that yearly variation in juvenile survival caused by characteristics of offspring and environmental conditions can be modulated by juvenile development and maternal effects, as proposed by Bernardo (1996) and Mousseau et al. (2009). Local selective pressures that can modify the influence of certain care or play behaviors on offspring survival could lead to behavioral specifications across populations of the same species (Berger 1979). Importantly, we showed that maternal care and juvenile development have a direct and hence stronger influence on offspring survival than maternal traits and environmental conditions. Since variation in offspring survival is a fundamental determinant of population dynamics, behavioral components of maternal care and juvenile play thus have greater implications on population dynamics than previously believed. Our results therefore illustrate that these two determinants, which are too often neglected in studies on offspring survival in mammals, should be given greater consideration.

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