Getting fat or getting help? How female mammals cope with energetic constraints on reproduction

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Abstract

Background: Fat deposits enable a female mammal to bear the energy costs of offspring production and thus greatly influence her reproductive success. However, increasing locomotor costs and reduced agility counterbalance the fitness benefits of storing body fat. In species where costs of reproduction are distributed over other individuals such as fathers or non-breeding group members, reproductive females might therefore benefit from storing less energy in the form of body fat.

Results: Using a phylogenetic comparative approach on a sample of 87 mammalian species, and controlling for possible confounding variables, we found that reproductive females of species with allomaternal care exhibit reduced annual variation in body mass (estimated as CV body mass), which is a good proxy for the tendency to store body fat. Differential analyses of care behaviours such as allonursing or provisioning corroborated an energetic interpretation of this finding. The presumably most energy-intensive form of allomaternal care, provisioning of the young, had the strongest effect on CV body mass. In contrast, allonursing, which involves no additional influx of energy but distributes maternal help across different mothers, was not correlated with CV body mass.

Conclusions: Our results suggest that reproducing females in species with allomaternal care can afford to reduce reliance on fat reserves because of the helpers’ energetic contribution towards offspring rearing.

Keywords: Allomaternal care, Cooperative breeding, Body fat, Paternal care, Helping behaviours, Reproduction, Allonursing, Provisioning

Background

Reproduction is energetically very expensive [1, 2] and several studies show that the amount of food available and hence the total amount of energy invested by the mother influences reproductive success in female mammals. Provisioning by humans generally leads to higher reproductive rates, shorter lactation periods, and shorter inter-birth intervals [3–5]. In natural animal populations, higher food abundance leads to higher birth rates [6–11]. In contrast, food restriction may delay sexual maturation and among adults may inhibit mating behaviour [12–14] or even produce acyclicity or anoestrus [15, 16].

In mammals that evolved in seasonal environments and thus face periods of food scarcity, a female’s ability to bear the energy costs of pregnancy and lactation, and thus her reproductive success, may be affected by the amount of body fat she can deposit. That stored body fat plays an essential role in female reproduction has been proposed previously within the capital-income-continuum concept (for a review see [17]) and empirical evidence for this idea is abundant. For instance, in rhesus macaques (Macaca mulatta) and moose (Alces alces), the size of maternal fat stores positively affects pregnancy and birth rates [18, 19]. Furthermore, numerous studies show that heavier and fatter mothers produce heavier offspring that grow faster and are more likely to survive, suggesting that females in better body condition are able to allocate more stored resources to reproduction [20–25]. Finally, several studies in seals show that body fat is essential for lactation as seal
mothers lose more than 50% of their stored body fat until the end of lactation ([26] and references therein). Significant seasonal fattening in females may also be found if they do not reproduce, e.g. to buffer environmental food fluctuations [27, 28]. However, because reproductive seasons and experienced seasonality in food intake are generally interrelated, it is usually impossible to disentangle these two reasons for body fat storage [29–33]. Female polar bears (*Ursus maritimus*) offer an extreme example of this. They store body fat to hibernate due to adverse environmental conditions for up to 8 months while simultaneously meeting the nutritional demands of gestation and lactation during this fasting period [23].

But the positive effect of fat stores on fitness is counterbalanced by their costs. Large fat reserves increase the energy costs of locomotion due to higher body weight [34–37], and also reduce agility and speed and so may compromise fitness by increasing predation risk or decreasing hunting success [38–42]. Furthermore, in arboreal species, body fat may also impede terminal branch feeding [43]. Indeed, arboreal species are less prone to store fat than terrestrial ones [44]. Therefore, we hypothesize that female mammals should minimize the amount of fat stores if they have an alternative to fuel their reproductive success.

All other things being equal, the energetic burden of reproduction on reproductive females is reduced when the costs of reproduction are distributed over several individuals. Thus, in species where other individuals provide energetic costly allomaternal care behaviours, breeding females might need to store less energy in the form of body fat themselves and could avoid the locomotion and predation costs resulting from high amounts of body fat. Allomaternal inputs are found in many mammals, comprising behaviours such as provisioning, carrying, huddling or communal nesting, babysitting, and protection from predators or defence of resources against conspecifics. The effects of such allomaternal care on offspring survival or fertility have been demonstrated within and between species [45–51]. One likely mechanism underlying this effect is load-lightening of pregnant or lactating females by helpers (‘load-lightening’ hypothesis [52]) which has been demonstrated in meerkats [53], callitrichids [54, 55] and siamangs [56]. This load-lightening effect has also been demonstrated in some species with facultative helping, where females can rear their pups solitarily, but under certain conditions share care for the young with one or more additional individuals. For instance, female prairie voles (*Microtus ochrogaster*) and pine voles (*Microtus pinetorum*) had shorter interlitter intervals in family groups consisting of the breeding pair and former offspring compared to families without previous offspring [57, 58]. In striped mice (*Rhabdomys pumilio*) living in the succulent karoo, offspring grew faster when the father was present, which may indirectly benefit females when young are weaned earlier [59]. In females of a facultatively cooperative breeding bird species, the splendid fairy-wren (*Malurus splendidus*), the presence of helpers has been shown to increase survival of the breeding females and reduce the time for these females to renest after a brood [60]. Lastly, in another facultative cooperative breeder, the western bluebird (*Sialia mexicana*), the presence of helpers allowed the breeding female to lower her feeding rate, while nestlings still received more feeds at nests with helpers compared to nests without helpers present [60]. In sum, there is ample empirical evidence that distributing the costs of reproduction over two or more individuals yields an energetic benefit for mothers or offspring. We do not distinguish between the two, as a net fitness effect can be obtained by either.

Allonursing, the nursing of non-filial offspring, is another form of care that has been observed in every major mammalian lineage [61, 62]. However, allonursing events within a species are generally rare. For instance, in tufted capuchin monkeys (*Sapajus nigritus*) allosucking accounted for 13% of all sucking events [63], in South American fur seals (*Arctocephalus australis*) for around 3% [64], and in red deer calves (*Cervus elaphus*) allosucking was even less common [65]. Furthermore, the rejection rates of sucking of non-filial offspring are high. In guanacos (*Lama guanicoe*), for example, the rejection rate to non-filial offspring nursing attempts was three times higher than the rejection rate to filial nursing attempts [66]. Although allonursing may confer social benefits to the allonursed young [63, 67], the energetic benefits for offspring or mother are unclear. First, allonursing is more likely to occur when several females breed concurrently [62] and hence all females simultaneously bear the costs of reproduction. Therefore, the idea that allonursing functions as load-lightening mechanism for lactating females cannot apply [68], and instead allonursing may serve to more evenly divide maternal energy investment across different mothers [69]. Second, several studies show no apparent energetic benefits of allonursing for recipient offspring and/or mothers. For instance, red deer calves sucking only from maternal hinds increased faster in body weight than calves sucking maternal and non-maternal hinds [65]. Another study found no evidence that allonursing provides benefits to meerkat pups (*Suricata suricatta*) or mothers [70]: pups that received allonursing were not heavier at emergence and did not have a higher survival rate than pups that did not receive allonursing. Mothers whose litters were allonursed were not in better physical condition, did not re-conceive faster and did not reduce their own nursing investment compared to mothers who nursed their litters alone. To sum up, allonursing does not necessarily provide energetic benefits for the mother or offspring.
With the exception of allonursing, all other allomaternal care behaviours can be performed by all sorts of helpers in cooperatively breeding species, including fathers or non-breeding group members. Whereas the help provided by adult males (potential fathers) might be unaffected by their body condition [71] or food abundance [72], other non-breeding group members generally adjust their helping efforts in relation to their body condition. Furthermore, subordinates can also start to breed themselves, in which case their help to the dominant female could end abruptly or be minimal to begin with [73, 74]. These results suggest that paternal care is more reliable and thus more important for females than the help of others. On the other hand, in cooperative breeders more helpers than just the father might be around to take over the energetic costs of female reproduction. The optimum amount of body fat stored by a female may therefore vary depending on whether they receive no care, paternal care or additional help from several non-breeding group members.

The aim of this study is to test whether energetic contributions towards offspring rearing through costly care allow reproductive females to reduce the amount of energy (stored as body fat) they themselves need to invest. As a proxy for the seasonal tendency to store body fat, we use data on seasonal body mass variation within a year, the coefficient of variation (CV) in body mass, which has been shown to correlate with the amount of body fat within [44] and across species (PGLS: $P = 0.03, N = 8, \lambda = 0, R^2 = 0.56, \beta = 0.19, S.E. = 0.07, t = 2.74$, calculated from data in [44]). Compared to single body fat values obtained from cadavers, CV body mass captures seasonal fluctuations, allows for a larger sample size for each species and can also be collected for wild animals [75]. In total, both reliable information on the nature and extent of allomaternal help and sufficient data on annual variation in body mass was available for 87 species from 9 mammalian orders.

We expect that an increased energetic contribution in the form of allomaternal care provided by the male or non-breeding group members is negatively correlated with annual variation in body mass in females, because storing fat and allomaternal subsidies independently stabilize the energetic costs for female reproduction. To test this prediction, we explore the effect of different types of allomaternal help on annual body mass variation in females. On the other hand, we do not expect a correlation between allonursing behaviour and annual variation in body mass in females.

**Methods**

**CV body mass as a proxy for the tendency to store body fat**

In mammals, body fat explained between 41 and 92% of the intraspecific variation in body mass, the amount of body fat was highly correlated with carcass weight for each age and sex; hence body weight was a good predictor of total body fat (for a summary, see references in [44]). We therefore used seasonal changes of body mass over a year as a proxy for the tendency to store body fat. For a given species, we calculated the coefficient of variation (CV = standard deviation/mean) over monthly means of adult female body mass, yielding a total sample of 87 mammalian species from 9 orders (Additional files 1 and 2). In a previous study we validated the use of CV body mass as a proxy for variation in body fat by showing that the monthly body mass correlated with percentage body fat in several studies that measured both in the same specimens [44].

We compiled monthly body mass data from the literature, including only those studies that reported monthly mean body mass for at least 4 months per year. If body mass data were given for four seasons, pooled across several months (e.g., spring, summer, autumn and winter), we set the number of months sampled to four (16 studies). In most species, monthly mean body mass data was distributed evenly across the year, except for *Antechinus stuartii*, *Lycaon pictus*, *Spermophilus franklinii* and *Zapus hudsonicus*. If several sources were available for one species, preference was given to the study with the largest sample size conducted in the wild.

**Allomaternal care behaviours**

In quantifying allomaternal care behaviour, we followed Isler and van Schaik [76] to obtain continuous data on the frequency of occurrence of the following care behaviours: provisioning, carrying, protection and a variable that comprises other energetically influential care behaviours such as huddling, communal nesting and pup retrieval (see Additional file 3 for a detailed description of the classification protocol). As the sample in [76] was restricted to species with known brain size, we expanded it by an additional 30 species for which data on both CV body mass and allomaternal care behaviour was available in the literature (Additional files 1 and 2). In total, CV body mass and data on allomaternal care behaviour were available for 87 species. We did not compile data for bats and cetaceans because reliable data on allomaternal care of both cetaceans and bats are notoriously difficult to obtain. Moreover, the amount of body fat and hence CV body mass as a proxy for the tendency to store body fat in these two groups may underlie different constraints than in other mammals [44, 77–79], precluding predictions for a combined sample.

In addition, to distinguish the effects of allomaternal care provided by males (paternal care) from that provided by other group members (care by others) we summed up the frequency of occurrence of all allomaternal care behaviours separately for the father and other
group members. To investigate whether the results reported in this study are robust with respect to different coding schemes of allomaternal care, we additionally conducted all analyses by using a binary classification of all allomaternal care behaviours, with 1 indicating the presence and 0 the absence of the helping behaviour. Finally, we also conducted additional analyses with a binary classification of allomaternal care provided by males (paternal care) and that provided by other group members (care by others) (data from [76, 80, 81]).

Covariates
As captivity might affect body mass variation (for instance, under good husbandry conditions, most animals gain weight in captivity [82]), we added provenance (wild = 1/captivity = 0) as an additional factor in all analyses. Furthermore, we analysed the subsample of studies including only wild-caught females separately.

In a previous study we found that substrate use (arboreal versus terrestrial) influenced the amount of body fat of a species [44]. We therefore added substrate use as an additional factor in all analyses. Data from published sources were used to assign each species to one of two substrate use categories, terrestrial (0) or arboreal (1), based on their main habitat. Species were classified as terrestrial when they spent more than 50% of observation time on the ground ([83–86], see Additional file 1).

We also controlled for several other potential methodological confounds. First, some studies include body mass data from pregnant and lactating females in the population mean, which may artificially increase annual mass data from pregnant and lactating females in the study. As captivity might affect body mass variation (for instance, under good husbandry conditions, most animals gain weight in captivity [82]), we added provenance (wild = 1/captivity = 0) as an additional factor in all analyses. Furthermore, we added the number of months sampled as a covariate. Ideally, we would have preferred to use only those studies from the wild that reported the mean body mass for 12 consecutive months. However, in contrast to studies in captivity, most body mass data of wild living mammals have been recorded less frequently. Third, to control for allometric effects of size, we performed all analyses including log-transformed mean body mass as a covariate. Finally, as variation in female body mass may be influenced by life history traits such as litter size, neonatal mass, and the duration of gestation and lactation, we also included those as potential covariates.

Statistical analyses
Statistical analyses were done in JMP™ 12.0 [87] and in R3.1.3 [88]. In most species that exhibit allomaternal care, various kinds of care behaviours are observed, potentially resulting in collinearity problems in the statistical analyses. We checked this by generating variance inflation factors (VIF) to assess potential multicollinearity in the full set of allomaternal care behaviours [89, 90] using non-phylogenetic generalized linear models and the function “vif” (“car” package: [91]) in R. VIFs quantify how much the variance of an estimated model parameter is increased because of multicollinearity between predictors. The VIF for carry by the male, carry by others, provisioning by the male and provisioning by others was higher than 5, which indicates a problematic amount of covariance among predictors [92]. To solve this, we summed up the frequency of occurrence of carrying by the male and by others to one single variable “carrying” and similarly provisioning by the male and provisioning by others to “provisioning”. After this, the VIF of all allomaternal care behaviours in all models were less than 4, which indicates an acceptable amount of covariance among predictors (Additional file 4: Tables S1 and S2). Two life history traits (duration of gestation and neonatal mass) also showed VIFs consistently larger than 5 in all models (Additional file 4: Tables S1 and S2). To reduce the problematic multicollinearity in these models, we followed the method described in [93]: we first removed the life history variable with the highest VIF value from the models, the duration of gestation, and recalculated VIFs for the reduced models. Then, we removed neonatal mass, as it still had a VIF larger than 5. All remaining variables had VIFs lower than 5. We then repeated the analyses with the same specifications as the main analysis with these “reduced models” and assessed the relative contribution of each independent variable as described below.

We built phylogenetic generalized least-squares regressions (PGLS) models [94, 95] using the “caper” package [96] in R. Caper estimates PGLS model parameters in maximum likelihood [96] and the parameter lambda (λ), which quantifies the magnitude of the phylogenetic signal in the model residuals [94]. The value of λ can vary between 0, indicating no phylogenetic signal, and 1, indicating that the observed pattern fits a Brownian motion model of trait evolution along the branches of the phylogeny such that similarity between species is directly proportional to relatedness [94]. The phylogeny was based on a composite supertree from [97] (Additional file 5: Figure S1). CV body mass (used as a proxy for body fat) was the dependent variable, while measures of allomaternal care and all possible confounding variables (substrate use, provenance [wild / captivity], number of months sampled, inclusion of reproductive females, mean body mass and several life history variables) were independent variables in the PGLS models. We did not log-transform CV body mass values prior to the analysis as this would not have improved the skew of its distribution. Although the predictor CV body mass was skewed
towards smaller values, the distribution of the residuals of the PGLS models were normally distributed and did not comprise any outliers.

We used a model selection approach based on the AICc (Aikaike Information Criterion with correction for finite sample size, [98]) to determine the most important allomaternal care behaviours for female CV body mass. We ran the model selection across all possible models built with the explanatory variables mentioned above. We accounted for uncertainty in the models by performing model averaging [99] in the candidate model set including models with ΔAICc <2 [100]. ΔAICc is the difference in AICc between the focal model and the AICc of the best-fitting model in the candidate model set. Estimates of each parameter were averaged across the candidate models (means were weighted by the Akaike weight of a given model). The relative importance of a predictor was obtained by summing the Akaike’s weights of the models in the candidate model set including the focal predictor, following the method described by Symonds and Moussalli [101]. The method to perform model averaging with the PGLS function in the package “caper” [96] is described in [102] and the corresponding material is available at http://www.mpcm-evolution.org.

Results
The results confirmed our two main predictions. Model selection and averaging showed that the most important effect among allomaternal care behaviours on female CV body mass was provisioning of the young by the male and other group-members (Relative importance = 1) (Table 1, Fig. 1a). This form of allomaternal care was negatively correlated with CV body mass in reproductive females, suggesting that an energetic contribution towards offspring rearing allows females to reduce the amount of stored body fat. In contrast, allonursing, which involves no additional influx of energy but distributes maternal help across different mothers, did not correlate with CV body mass (Relative importance = 0.06) (Table 1). Results using a binary coding scheme of allomaternal care behaviours are strikingly similar (Additional file 4: Table S6 and S8, Fig. 1b).

Using a continuous coding scheme of paternal care and the amount of allomaternal care provided by other group members, we found that only paternal care showed a negative relationship with CV body mass (Relative importance = 1) (Table 2, Fig. 2a and b). In contrast, using a binary coding scheme, both paternal care and the amount of allomaternal care provided by other group members had a negative effect on CV body mass, although the negative effect of paternal care was stronger than that of allomaternal care by other group members (Additional file 4: Table S7 and S9, Figure S2a and b).

Results for the subset of studies including only wild-caught females (N = 49 species) were largely similar to those obtained from the whole sample, although the effects were a bit weaker (Additional file 4: Tables S10-S15).

### Table 1

Continuous classification of allomaternal care behaviours: Averaged parameter estimates and their relative explanatory importance for female CV body mass (N = 87). Gestation length and neonatal mass were excluded to reduce multicollinearity between predictors. Numbers in bold indicate predictors whose confidence intervals of their effect exclude zero

| Predictors                  | Relative importance of predictors | Model averaging estimates | 95% CI       |
|-----------------------------|----------------------------------|---------------------------|--------------|
| Intercept                   | 0.126                            | -0.040                    | (0.100, 0.153)|
| Provisioning                | 1.00                             | -0.040                    | (–0.043, –0.036)|
| Protecting                  | 0.06                             | -0.001                    | (–0.002, 0.001)|
| Carrying                    | 0.07                             | 0.003                     | (–0.004, 0.010)|
| Communal nesting            | 0.06                             | 0.001                     | (–0.002, 0.004)|
| Allonursing                 | 0.06                             | 0.005                     | (–0.010, 0.021)|
| Log mean body mass          | 0.44                             | -0.006                    | (–0.010, –0.002)|
| Provenance                  | 0.80                             | na                        | na           |
| Wild                        | 0.25                             | na                        | na           | (0.017, 0.032)|
| Substrate use               | 1.00                             | na                        | na           |
| Terrestrial                 | 0.78                             | na                        | na           | (–0.050, –0.041)|
| Arboreal                    | 0.69                             | -0.019                    | (–0.001, 0.001)|
| Number of months            | 0.53                             | -0.001                    | (–0.019, –0.008)|
| Inclusion of reproductive females | 0.56                           | 0.027                     | (0.013, 0.041)|
| Log litter size             | na                               | 0                         | 0            |

*averaged model estimates based on 12 models with ΔAICc (AICc focal model – AICc best model) < 2 since the best AICc model is not strongly weighted (weight = 0.15) [104]. A full list of models is given in Additional file 4: Table S4. Reference levels of categorical variables have an estimate of 0; na – not applicable; 95% CI - 95% confidence interval
In all analyses substrate use and provenance were correlated with CV body mass. Arboreal species had less body fat than terrestrial and semiaquatic species, as indicated by the negative correlation between CV body mass and substrate use. Furthermore, CV body mass was higher in wild-caught specimens compared to captive ones, suggesting that wild-caught individuals experience more variation in energy intake than provisioned specimens living in captivity. Controlling for further possible confounding variables (number of months sampled, inclusion of reproductive females, mean body mass, and several life history variables) did not change the effects of the main explanatory variables. In some models, both a lower species body mass and the inclusion of reproductive females in the study were related to a lower CV body mass, while species with a relatively high reproductive rate, as indicated by larger litters, exhibited a higher CV body mass. In some models, species for which fewer months were sampled showed a larger CV body mass (Tables 1 and 2 and Additional file 4: Tables S6, S7, S12 and S13).

**Discussion**

Using annual variation in body mass, we found that this CV body mass and the amount of allomaternal care show a pattern of correlated evolution among female mammals: females of those species with more contributions of non-mothers to offspring care exhibit reduced annual variation in body mass. From this, we conclude that allomaternal energy subsidies and fat storage are compensatory strategies to stabilise the energetic costs involved in female reproduction.

**Table 2** Continuous classification of paternal care and care provided by other group members: Averaged parameter estimates and their relative explanatory importance for female CV body mass (N = 87). Gestation length and neonatal mass were excluded to reduce multicollinearity between predictors. Numbers in bold indicate predictors whose confidence intervals of their effect exclude zero. Numbers in bold indicate predictors whose confidence intervals of their effect exclude zero.

| Predictors                | Relative importance of predictors | Model averaging estimates | 95% CI     |
|---------------------------|----------------------------------|---------------------------|------------|
| Intercept                 | 0.148                            | 0.148                     | (0.127, 0.169) |
| Care by others            | na                               | 0                         | 0          |
| Paternal care             | 1.00                             | -0.028                    | (-0.029, -0.027) |
| Log mean body mass        | 0.67                             | -0.008                    | (-0.011, -0.004) |
| Provenance                | Captive                         | 0.80                      | na         |
|                           | Wild                             | 0.024                     | (0.017, 0.032) |
| Substrate use             | Terrestrial                      | 1.00                      | Na         |
|                           | Arboreal                        | -0.047                    | (-0.050, -0.043) |
| Number of months          | 0.38                             | -0.001                    | (-0.002, -0.001) |
| Inclusion of reproductive females | 0.37                             | -0.011                    | (-0.020, -0.002) |
| Log litter size           | 0.24                             | 0.007                     | (-0.001, 0.016) |
| Log weaning age           | na                               | 0                         | 0          |

*averaged model estimates based on 11 models with ΔAICc (AICc_focal model - AICc_best model) < 2 since the best AICc model is not strongly weighted (weight = 0.15) [104]. A full list of models is given in Additional file 4: Table S5. Reference levels of categorical variables have an estimate of 0; na – not applicable; 95% CI - 95% confidence interval
First, we predicted that only an additional influx of energy in the form of costly allomaternal care behaviours by the male and other non-breeding group members towards the offspring and the mother would allow reproductive females to reduce the storage of body fat, whereas a mere redistribution of energy between mothers as in allonursing behaviour would not. As predicted, we only found a negative correlation between seasonal variation in body mass and the amount of allomaternal care in the form of provisioning of the young by the male and other group members, but not with allonursing. This suggests that if other conspecifics take over some of the maternal costs the need for these females to store extra body fat to fuel reproduction is relaxed.

This pattern across species is consistent with numerous intra-specific studies showing that extra energy delivered by costly care behaviours of helpers allows breeding females to reduce their maternal investment. For instance, in meerkats and cooperatively breeding bird species, an increased number of helpers enabled breeding females to maintain better condition and higher body mass and achieve a higher fitness [103–107]. In Campbell’s dwarf hamsters (Phodopus campbelli) the presence of males protects females against extreme heat production in response to the exogenous heat requirements of the pups. As this acute increase in maternal temperature is thought to be a substantial cost to females, paternal presence likely allows females to decrease the energetic demands of reproduction [108].

Another study of the same species found that removal of the male not only decreased pup survival, growth, and readiness for dispersal by 18 days of age but also resulted in an additional 20% body weight loss in the female [109]. Lastly, a comparative study across mammals reveals that male care is associated with larger litters in some species or shorter lactation time in others, resulting in increased female fecundity [51].

Second, we investigated the effect of different types of allomaternal help (help of the male or other conspecifics) on female fat stores. Both the help provided by the breeding male and the help provided by other group members showed a negative correlation with female CV body mass. However, the relative importance of allomaternal care provided by the breeding male was greater than the relative importance of help of other caretakers. This fits well with the often-reported finding that males care unconditionally, whereas care by helpers may be more conditional [71, 72, 110].

A broad comparative study as presented here can only provide an overview over potential patterns of correlated evolution and is limited by methodological issues. Ideally, we would have preferred to use individual variation in body fat over the year instead of the annual variation in body mass averaged over several females as used in this study. Although the published literature contains a variety of measures of adipose depots in living subjects such as palpation, skinfold thickness, perirenal adiposity, the number of adipocytes in bone marrow, and adipocyte volumes from tissue samples [111], these measures have not yet been compared to each other and each measure has only been applied to very few different species making broad phylogenetic comparisons impossible. Similarly, taking body fat values obtained from cadavers is problematic because they assess body fat at a single point in time, while the individual body fat fluctuations remain unknown [73].

It may be argued that, rather than taking annual variation in body mass, the costs of reproduction should be estimated by subtracting the maternal body weight at conception from the body weight at offspring weaning. However, such detailed data are rarely available, and may raise other issues, such as postpartum oestrus in lago-morphs, Callitrichid primates and several otariids, which means females suckle newborns while simultaneously being pregnant [112–115]. Even more importantly, in most mammals such as carnivores, rodents and primates allomaternal care and its beneficial effect for mothers continues post-weaning. Thus, offspring provisioning until independence allows females to invest more time in
foraging, regain body condition more quickly and mate sooner [116], which we would not capture with the body weight difference of mothers between conception and offspring weaning.

In our study, some part of the variation in female body mass may result from the increasing weight of the foetus or litter during gestation. However, without dissection this cannot be disentangled from storing energy reserves during gestation for the subsequent lactation period, which is even more energetically demanding [33]. As a rough control for such effects, we included neonatal mass, litter size, gestation length and lactation time as potential correlates in the analyses, but this did not alter our findings. Moreover, because cooperative breeders tend to have higher reproductive efforts than independent breeder [117], this possibility cannot explain the reduced CV in body mass among species receiving allomaternal care.

In our data, we found a surprisingly weak phylogenetic signal of CV body mass and thus low values of λ for the model residuals, indicating that the phylogenetic disposition for fat disposition is partially masked by habitat-caused variation [118–120]. The fact that we still found significant relationships between CV body mass and allomaternal care would then make our case even stronger, because it implies that the underlying effect must be very strong.

Another unsolved question concerns the relationship between reproductive effort, seasonal fluctuations in climate or food abundance, and social factors such as allomaternal care. Reproductive seasons and experienced seasonality in food intake are generally interrelated in mammals [30]. There is evidence that species inhabiting more seasonal and less predictable habitats more often breed cooperatively [121, 122], and we also expect that they would benefit more from a higher ability to store body fat. However, because we found a negative, rather than the expected positive correlation between allomaternal care and the tendency to store body fat, this confirms that there is indeed a trade-off due to energetic costs of fat storage, and thus that social and physiological buffers are compensatory strategies to maintain fitness in a harsh environment. To further investigate these strategies, we would not only need data on environmental factors such as annual rainfall, vegetation indices or actual food abundance, but also of the seasonality experienced by the animals themselves, as expressed in dietary habits throughout the year, analogous to our studies of brain size and seasonality in primates [123–125].

Conclusions

In conclusion, several lines of evidence suggest that any allomaternal care, be it aimed at the mother or the offspring, and be it by the father or other conspecifics, allows females to reduce the amount of stored body fat. In combination with intraspecific studies, our results further support the idea that the main reason for this negative correlation between the amount of allomaternal care and female CV body mass is the energetic contribution towards offspring rearing through costly care by males or helpers, which stabilises the energetic costs for female reproduction. Although our comparative approach has some limitations, our analyses indicate that female mammals have two different strategies of coping with energetic constraints on reproduction: either getting fat or getting help.

Additional files

- **Additional file 1**: List of species and data used for this study. (XLSX 22 kb)
- **Additional file 2**: References for the CV body mass data used for this study. (DOCX 60 kb)
- **Additional file 3**: Compilation and quantification of allomaternal care behaviours. (DOCX 37 kb)
- **Additional file 4**: Supplementary results: Tables S1 and S2. Results testing for collinearity among predictors. Variation inflation factors (VIF) for all the full models and all the reduced models after multicollinearity is considered. Table S3. Estimated phylogenetic signal (λ) in the individual variables. Tables S4 and S5. Model sets obtained after model selection based on ΔAICc <2 including best-supported models and multiple-model parameter estimates. Tables S6-S9 and Figure S2. Results of a binary coding scheme of allomaternal care behaviours as well as binary coded care provided by males (paternal care) or other group members (care by others). Tables S10-S15. Results for the subset of studies including only wild-caught females (N = 49). These remained largely identical to those obtained with the whole dataset (see also Tables 1 and 2 in the main text). (DOCX 163 kb)
- **Additional file 5**: Phylogenetic tree of 87 mammal species used in this study visualised using Mesquite v. 3.11 [126]. (PDF 83 kb)

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Availability of data and materials

The dataset and all additional analyses supporting the conclusions of this article are available in the supplementary information files.

Authors’ contributions

SAH collected the data, performed the statistical analyses and wrote the paper. CVS and KI co-wrote the manuscript. All authors contributed to the design of the study, discussed the results and gave final approval for publication.

Competing interests

The authors declare that they have no competing interests.

Consent for publication

Not applicable.
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References
1. McNab BK. The energetics of reproduction in endotherms and its implication for their conservation. Integr Comp Biol. 2006;46:1159–68.
2. Speakman JR. The physiological costs of reproduction in small mammals. Phil Trans R Soc B. 2008;363:375–9.
3. Mori A. Analysis of population changes by measurement of body weight in the Koshimla troop of Japanese monkeys. Primates. 1979;20:371–97.
4. Küster J, Paul A. Female reproductive characteristics in semi-free-ranging Barbary macaques (Macaca sylvanus L. 1758). Folia Primatol. 1984;43:69–83.
5. Borres C, Koenig A, Winkler P. Variation of life history traits and mating patterns in female langur monkeys (Semnopithecus entellus). Behav Ecol Sociobiol. 2001;53:291–402.
6. Tyler NIC. Natural limitation of the abundance of the high arctic Svalbard reindeer. Cambridge. University of Cambridge; 1987.
7. Wauters LA, Lens L. Effects of food availability and density on red squirrel (Sciurus vulgaris) reproduction. Ecology. 1995;76:2460–9.
8. Heesen M, Rogahn S, Otter J, Schülke O. Food abundance affects energy intake and reproduction in frugivorous female Assam macaques. Behav Ecol Sociobiol. 2013;67:1053–66.
9. Takahashi H. Female reproductive parameters and fruit availability: factors determining onset of estrus in Japanese macaques. Am J Primatol. 2002;57:141–53.
10. Arlett ME, Isbell LA, Kastik A, Møller F, Chancellor RL, Chapman CA, et al. Determinants of reproductive performance among female grey-cheeked mangabeys (Lophocebus albigena) in Kibale National Park, Uganda. Int J Primatol. 2015;36:65–73.
11. van Noordwijk MA, van Schaik CP. The effects of dominance rank and group size on female lifetime reproductive success in wild long-tailed macaques, Macaca fascicularis. Primates. 1999;40:105–30.
12. Gill CJ, Rissman EF. Female sexual behavior is inhibited by short-and long-term food restriction. Physiol Behav. 1997;61:387–94.
13. Temple JL, Schneider JE, Scott DK, Konotz A, Rissman EF. Mating behavior is controlled by acute changes in metabolic fuels. Am J Physiol Regul Integr Comp Physiol. 2002;282:R782–90.
14. Cowlishaw G, Dunbar RI. Population biology. In: Cowlishaw G, Dunbar RI, editors. Primate Conservation biology. Chicago: University of Chicago Press; 2000. p. 119–53.
15. Wade GN, Schneider JE. Metabolic fuels and reproduction in female mammals. Neurosci Biobehav Rev. 1992;16:235–72.
16. Kauffman AS, Bokwoksa K, Rissman EF. Critical periods of susceptibility to short-term energy challenge during pregnancy: impact on fertility and offspring development. Physiol Behav. 2010;99:100–8.
17. Jonsson KI. Capital and income breeding as alternative tactics of resource use in reproduction. Oikos. 1997;78:57–66.
18. Campbell BC, Gerald WS. Body composition, age and fertility among free-ranging female rhesus macaques (Macaca mulatta). J Med Primatol. 2004;33:70–7.
19. Testa JW, Adams GP. Body condition and adjustments to reproductive effort in female moose (Alces alces). J Mammal. 1998;79:1345–54.
20. Rödel HG, Valencak TG, Handrek A, Monclus R. Paying the energetic costs of reproduction: reliance on postpartum foraging and stored reserves. Behav Ecol. 2016;27:748–56.
21. Lewis RJ, Kapper PM. Seasonality, body condition, and timing of reproduction in Propithecus verreauxi verreauxi in the Kirindy Forest. Am J Primatol. 2005;67:347–64.
22. Coté SD, Festa-Bianchet M. Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. Oecologia. 2001;127:230–8.
23. Atkinson S, Ramsay M. The effects of prolonged fasting of the body composition and reproductive success of female polar bears (Ursus maritimus). Funct Ecol. 1995;9:559–67.

24. Christiansen F, Vikingsson GA, Rasmussen MH, Lusseau D. Female body condition affects foetal growth in a capital breeding mysticete. Funct Ecol. 2014;28:579–88.
25. Schneider JE, Wade GN. Effects of maternal diet, body weight and body composition on infanticide in Syrian hamsters. Physiol Behav. 1989;46:815–21.
26. Bowen WD, Oftedal OT, Bóness DJ. Mass and energy transfer during lactation in a small phocid, the harbor seal (Phoca vitulina). Physiol Zool. 1992;65:844–6.
27. Short HL, Duke WB. Seasonal food consumption and body weights of captive tree squirrels. J Wildl Manag. 1971;35:435–9.
28. Zhang Z-Q, Wang D-H. Seasonal changes in thermogenesis and body mass in wild Mongolian gerbils (Meriones unguiculatus). Comp Biochem Physiol A. 2007;148:346–53.
29. Batzli GO, Pitelka FA. Condition and diet of cycling populations of the California vole, Microtus californicus. J Mammal. 1971;52:141–63.
30. Bronson FH. Mammalian reproductive biology. Chicago: University of Chicago Press; 1989.
31. Tyler NIC, Blix AS. Survival strategies in Arctic ungulates. Rangifer. 1990;10:211–30.
32. Réale D, McAdam AG, Boutin S, Berteaux D. Genetic and plastic responses of a northerm mammal to climate change. Proc R Soc B. 2003;270:591–6.
33. van Schaik CP, van Noordwijk MA. Interannual variability in fruit abundance and the reproductive seasonality in Sumatran long-tailed macaques (Macaca fascicularis). J Zool. 1985;206:533–49.
34. Ekelund U, Aman J, Yngve A, Renman C, Westerterp K, Sjostrom M. Physical activity but not energy expenditure is reduced in obese adolescents: a case-control study. Am J Clin Nutr. 2002;76:935–41.
35. Garby L, Laroo JS, Jorgensen B, Lammert Q, Madsen K, Sorensen P, et al. Relation between energy expenditure and body composition in man – specific energy expenditure in vivo of fat and fat-free tissue. Eur J Clin Nutr. 1988;42:301–5.
36. Taylor CR, Heglund NC, Maloyy GWO. Energetics and mechanics of terrestrial locomotion. 1. Metabolic energy consumption as a function of speed and size in birds and mammals. J Exp Biol. 1982;297:1–21.
37. Peyrot N, Thivel D, Isacco L, Morin J-B, Duché P, Belli A. Do mechanical gait parameters explain the higher metabolic cost of walking in obese adolescents? J Appl Physiol. 2009;106:1763–70.
38. Pond CM. Morphological aspects and ecological and mechanical consequences of fat deposition in wild vertebrates. Annu Rev Ecol Evol Syst. 1979;5:519–70.
39. Hetz MW, Piersma T, Hedenstrom A, Brugge M. Intraspecific variation in avian pectoral muscle mass: constraints on maintaining manoeuvrability with increasing body mass. Funct Ecol. 2007;21:317–26.
40. Zamora-Camacho FJ, Reguera S, Rubino-Hispán MW, Moreno-Ruenda G. Effects of limb length, body mass, gender, gravity, and elevation on escape speed in the lizard Psammodromus algirus. Evol Biol. 2014;41:509–17.
41. Gosler AG, Greenwood JJD, Perrins C. Predation risk and the cost of being fat. Nature. 1995;377:621–3.
42. West DB, York B. Dietary fat, genetic predisposition, and obesity: lessons from animal models. Am J Clin Nutr. 1998;67:505S–12.
43. Dittus WPJ. Arboreal adaptations of body fat in wild toque macaques (Macaca sinica) and the evolution of adiposity in primates. Am J Phys Anthropol. 2013;152:333–44.
44. Heldstab SA, van Schaik CP, Iler K, Being fat and smart: a comparative analysis of the fat-brain trade-off in mammals. J Hum Evol. 2016;100:25–34.
45. Snowdon CT. Infant care in cooperatively breeding species. Adv Stud Behav. 1996;25:643–89.
46. Silk JB. The adaptive value of sociality in mammalian groups. Proc R Soc B. 2007;362:539–59.
47. Gittleman JL, Oftedal OT. Comparative growth and lactation energetics in carnivores. In: Gittleman JL, editor. Carnivore behavior, ecology, and evolution, vol. 1. Dordrecht: Springer; 1989. p. 355–79.
48. Moehlman PD, Hofer H. Cooperative breeding, reproductive suppression, and body mass in canids. In: Solomon NG, French JA, editors. Cooperative breeding in mammals. Cambridge: Cambridge University Press; 1997. p. 75–127.
49. Mistreni JC, Watts D. The evolution of non-maternal caretaking among anthropoid primates: a test of the hypotheses. Folia Primatol. 2000;71:93–113.
50. West HE, Capellini I. Male care and life history traits in mammals. Nat Commun. 2016;7:11854.
111. Ellis KJ. Human body composition: in vivo methods. Physiol Rev. 2000; 80:649–80.
112. Brambell F. The reproduction of the wild rabbit Oryctolagus cuniculus (L.). J Zool. 1944;114:1–45.
113. Trillmich F, Wolf JB. Parent–offspring and sibling conflict in Galápagos fur seals and sea lions. Behav Ecol Sociobiol. 2008;62:363–75.
114. French JA, Brewer KJ, Schaffner CM, Schalley J, Hightower-Meritt D, Smith TE, et al. Urinary steroid and gonadotropin excretion across the reproductive cycle in female Wied’s black tufted-ear marmosets (Callithrix kuhli). Am J Primatol. 1996;40:231–45.
115. Ziegler T, Widowski T, Larson M, Snowdon C. Nursing does affect the duration of the post-partum to ovulation interval in cotton-top tamarins (Saguinus oedipus). J Reprod Fertil. 1990;90:563–70.
116. Cantoni D, Brown RE. Paternal investment and reproductive success in the California mouse, Peromyscus californicus. Anim Behav. 1997;54:377–86.
117. Lukas D, Clutton-Brock T. Life histories and the evolution of cooperative breeding in mammals. Proc R Soc B. 2012;279:4065–70.
118. Hahn DA. Two closely related species of desert carpenter ant differ in individual-level allocation to fat storage. Physiol Biochem Zool. 2006;79:487–56.
119. Muehlenbein MP, Campbell BC, Richards RJ, Watts DP, Svec F, Falkenstein KP, et al. Leptin, adiposity, and testosterone in captive male macaques. Am J Phys Anthropol. 2005;127:335–41.
120. Harlow HJ. Fasting biochemistry of representative spontaneous and facultative hibernators: the white-tailed prairie dog and the black-tailed prairie dog. Phys Zool. 1995;68:8915–34.
121. Clutton-Brock T. Mammal societies. 1st ed. Chichester: John Wiley & Sons; 2016.
122. Lukas D, Clutton-Brock T. Climate and the distribution of cooperative breeding in mammals. R Soc Open Sci. 2017;4:160897.
123. van Woerden JT, van Schaik CP, Isler K. Brief communication: seasonality of diet composition is related to brain size in new World monkeys. Am J Phys Anthropol. 2014;154:628–32.
124. van Woerden JT, Willems EP, van Schaik CP, Isler K. Large brains buffer energetic effects of seasonal habitats in catarrhine primates. Evolution. 2012;66:191–9.
125. van Woerden JT, van Schaik CP, Isler K. Effects of seasonality on brain size evolution: evidence from strepsirrhine primates. Am Nat. 2010;176:758–67.
126. Maddison WP, Maddison DR. Mesquite: a modular system for evolutionary analysis. Version 3.11 http://mesquiteproject.org. 2017. Accessed 30 Mar 2017.