



# A milk-sharing economy allows placental mammals to overcome their metabolic limits

Paola Cerrito<sup>a,b,c,1,2</sup> and Jeffrey K. Spear<sup>a,b,1,2</sup>

<sup>a</sup>Department of Anthropology, New York University, New York, NY 10003; <sup>b</sup>New York Consortium in Evolutionary Primatology, New York, NY; and <sup>c</sup>Department of Molecular Pathobiology, New York University College of Dentistry, New York, NY 10010

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**Maternal resource availability and metabolism have a strong limiting effect on reproductive output. Allomaternal care and domestication increase the energy available to the mother and should correlate with an increase in reproductive output. Here, we take a comparative approach to understand how this increase is accomplished (e.g., litter mass, reproductive frequency, etc.) and the strength of the effect among different forms of external energetic supplementation. We find that domestication and all forms of allomothering correlate with increased fertility. All forms of provisioning correlate with larger litters without compromising offspring size. The greatest increase we observe in reproductive power is in species that practice allonursing. Our results suggest that the ultimate factor limiting reproductive output in placental mammals is maternal metabolic power rather than resource availability.**

alloparenting | domestication | life history | reproduction | allonursing

Organisms work as energy transformers (1). They take energy from the environment and differentially allocate it toward growth, maintenance, and reproduction in order to maximize their inclusive fitness (2). Resource availability helps drive a species' life history profile by imposing trade-offs between reproduction, growth, and maintenance (3), and it is well established that resource availability has limiting effects on the reproductive output of both mammals (4) and birds (5). Specifically, total energy consumption (from foraging plus any external provisioning) will equal the cost of growth, activity, basal metabolism, and reproduction (6) (which, in female mammals, must also include the growth, activity, and metabolism of a nursing infant) (*SI Appendix, Fig. S1*).

External provisioning, whether in the form of allomaternal care or domestication, increases the energy available to a mother and infant and/or decreases the energy necessary to allocate to foraging activities. If allomothering and domestication do not change the growth or basal metabolism of the mother, it follows that domestication and alloparenting should increase the energy a mother can allocate to reproduction.

Several species-specific studies (7) have assessed the effect of the presence of helpers (allomothers) on present or future reproductive output of breeding females, finding mixed support for an actual increase [e.g., increase (8–11); no increase (12–15)]. Alternatively, these mixed results could be explained by trade-offs between reproduction and metabolically expensive tissues such as brain size (16). Isler and van Schaik (16) argue that the evolution of allomothering in a lineage facilitates an evolutionary increase in either brain size, fertility, or both (albeit each to a lesser extent) depending on the identity of the alloparent.

Like allomothering, domestication represents an increase in energetic availability and is therefore thought to correlate with an increase in reproductive output. Species-specific studies have shown that domestication releases the constraint of seasonality in seasonal breeders (17), induces an earlier onset of sexual maturity (18–20), and correlates with an increased frequency of reproductive cycles (17, 21), concurrently contributing to an increase in reproductive output (22, 23). The similarities between domestication and allomothering present an opportunity to

use a comparative approach to address fundamental questions about the reproductive constraints imposed on mothers by both resource availability and maternal metabolism.

Here, we examine the relationship between domestication or several types of allomothering and different variables related to reproductive output (*SI Appendix, Table S1*) in placental mammals (the sample includes nearly all domesticated mammals as well as 445 taxa with allomothering data representing all placental orders) to understand how changes in the maternal energy budget affect life history strategies.

Specifically, a breeding female could improve her reproductive output through 1) changes to timing (earlier age at first birth, shorter interbirth interval [IBI], longer reproductive lifespan); 2) changes to each reproductive event (more offspring in each litter, larger offspring in each litter, or some combination thereof producing a greater total mass of a litter); or 3) changes to reproductive power (greater lifetime reproductive output, more infant mass produced per year). We make several predictions:

**Prediction 1:** Allomothering that involves the postweaning provisioning of the infant will have no effect on the timing of reproductive events, the nature of individual reproductive events, or reproductive power of the female. Since this provisioning occurs after weaning, it does not directly impact the mother's energy balance.

**Prediction 2:** Following previous literature (17), we predict that domesticated animals will exhibit earlier ages at first birth, shorter IBIs, and higher lifetime reproductive outputs. Domesticated species benefit from an increased food availability and reduced energy expenditure on nonreproductive activities such as locomotion, foraging, and defense throughout their entire life, allowing them to allocate more energy to reproduction (*SI Appendix, Fig. S1*).

## Significance

Here, we demonstrate that a naturally evolving behavior (allonursing) has greater effect on reproductive power (mass per unit of time) and output (litter mass at birth) than does artificial selection (domestication). Additionally, we demonstrate the importance of resource optimization afforded by sociality (rather than resource abundance per se) in shaping a species' life history profile and its ability to overcome its own physiological constraints.

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The authors declare no competing interest.

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<sup>1</sup>P.C. and J.K.S. contributed equally to this work.

<sup>2</sup>To whom correspondence may be addressed. Email: pc2294@nyu.edu or jks417@nyu.edu.

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**Prediction 3:** Domestication, allonursing, and allocare that replaces maternal energy expenditure (such as infant carrying and pup retrieval) will both increase the total mass of a litter (through increased neonate size, increased litter size, or both) and the offspring produced in a specific period of time (reproductive power). These forms of allocare allow the mother to allocate more resources to reproduction, giving her the opportunity to produce more or larger offspring with each litter.

**Prediction 3A:** In line with previous research that focused on the effects of different type of allocare on brain size (24), we predict that more-reliable forms of help for the mother, such as domestication, will be associated with larger infants, while less-reliable forms of help for the mother, such as allocare from others or allonursing, will be associated with larger litters.

**Prediction 4:** Since lactation is more metabolically demanding than gestation (25), we predict allonursing to have the strongest effect on reproductive power (mass produced per year), but overall lifetime reproductive output will nonetheless be higher for domesticated species, which benefit from a longer reproductive lifespan.

## Results

Of the 167 different models that we test, 21 show a statistically significant association between either domestication or allocare and one of the measures of reproductive output or metabolic function when using our more-conservative alpha level ( $P < 0.00625$ ; 32 in total had a  $P < 0.05$ ). When using raw neonatal litter masses or when raising the mass of neonates to the power of 0.75 to account for the nonlinear scaling of mass and energy requirements, the same models are significant, and the same models have the lowest Akaike Information Criterion (AIC). Considering the adjusted and nonadjusted models with neonatal mass to be the same hypothesis, we test 131 different models, and 15 are significant. We use the values for the adjusted variables throughout the text.

Domestication correlates with a significant increase in litter size ( $P < 0.0001$ ; Fig. 1), fertility ( $P < 0.0001$ ), neonatal litter mass ( $P = 0.00001$ ), lifetime reproductive output as litter mass over a lifetime ( $P < 0.000001$ ), and mass produced per year ( $P < 0.000001$ ). Allonursing is associated with a significant increase in litter size ( $P = 0.0007$ ), fertility ( $P = 0.0042$ ; Fig. 2), neonatal litter mass ( $P < 0.0001$ ), and mass produced per year ( $P = 0.0008$ ). Combined energetic input (infant provisioning plus allonursing) correlates with an increase in neonatal litter mass ( $P = 0.0008$ ). Infant provisioning by nonparent group members is associated with an increase in litter size ( $P = 0.0005$ ) and fertility ( $P = 0.0012$ ). Infant carrying by both males and alloparents correlates with a decrease in IBIs ( $P = 0.0018$ ) and an increase in fertility ( $P = 0.0057$ ). Infant carrying by alloparents only correlates with an increase in fertility ( $P = 0.0053$ ). Finally, neither basal metabolic rate nor total energy expenditure (TEE) are significantly different for domesticated species or species practicing alloparental care, although for domestication there are only three species with TEE data, so we excluded this model ( $TEE \sim \text{adult\_body\_mass} + \text{domestication}$ ) from further analyses and discussions. The 15 models that are significant are reported in Table 1 with associated  $P$  values, sample size, effect size, and the results of the AIC comparisons. For most response variables, the best-fit model based on AIC is also the significant model (if there is one) with the largest effect size. The two exceptions are lifetime reproductive output, where the only significant explanatory variable, domestication, has an AIC within 2 of several other models, including alloparental carrying, energy in, and allonursing, and fertility, where the best fit model, others provisioning, is not the model with the largest effect size. Results with a  $P < 0.05$  (but  $>0.00625$ ) are reported in *SI Appendix, Table S3* along with all

models that had  $P > 0.05$  but AIC scores within 2 of the model with the lowest AIC; results of all 167 models are reported in the *Dataset S4*; AIC weights of all model comparisons are reported in *Dataset S5*.

**Prediction 1:** Provisioning after weaning will have no impact on the mother's reproductive timing, events, or power. Prediction 1 is mostly contradicted by our results, with provisioning by others (but not by males) being correlated with both an increase in litter size and an increase in fertility

**Prediction 2:** Domesticated animals will have earlier age at first birth, shorter IBIs, and higher lifetime reproductive output. Prediction 2 is partially supported by our results, with lifetime reproductive output being higher only in domesticated species. However, age at first birth and IBIs are not significantly reduced.

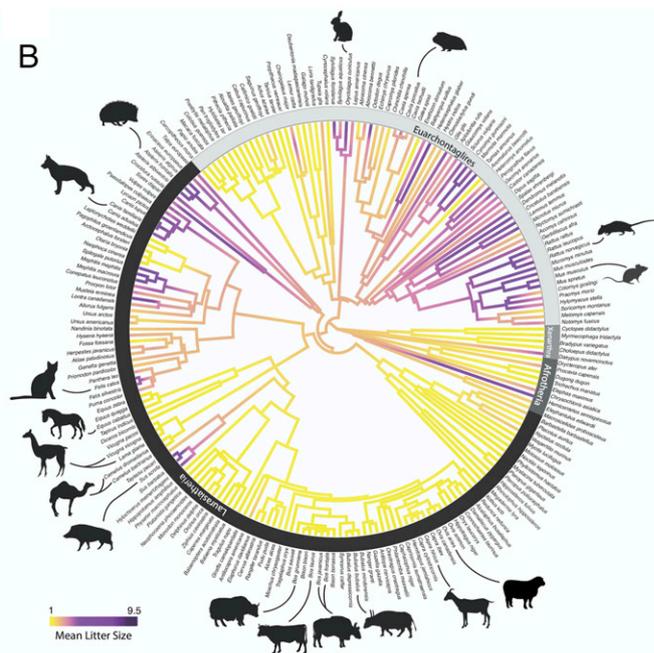
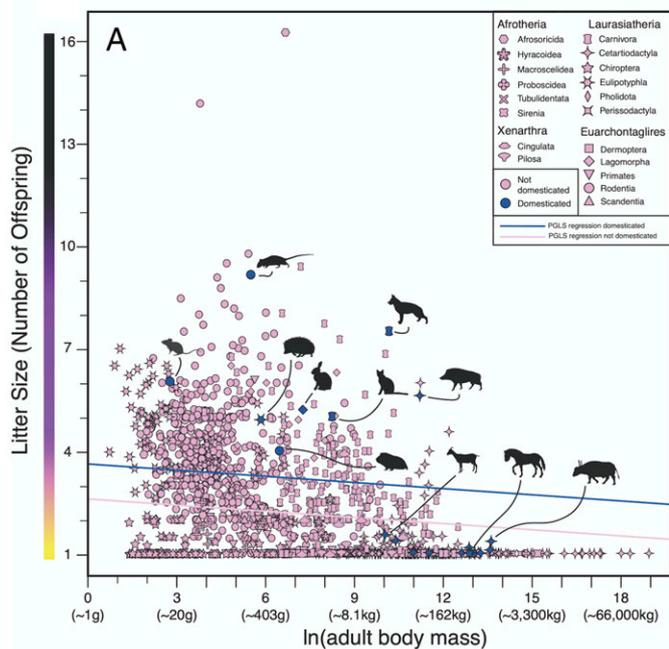
**Prediction 3:** Domestication, allonursing, and allocare (carrying, etc.) will increase the total mass of offspring in each litter as well as reproductive power. Prediction 3 is largely supported by our results, with both domestication and allonursing correlating with an increase in litter size, neonatal litter mass (Fig. 3), fertility, and mass produced per year. Additionally, both infant carrying by alloparents only and by alloparents and males combined correlate with a significant increase in fertility.

**Prediction 3A:** More-reliable forms of help for the mother will be associated with larger infants, while less-reliable forms of help for the mother will be associated with larger litters. Prediction 3A is mostly supported by our results, as an increase in litter size is associated with both reliable and unreliable help: domestication, provisioning by alloparents, and allonursing. In support of our prediction, the effect size is strongest for the source that is likely least reliable (allonursing; +1.3 infants per litter) and weakest for the source that is likely most reliable (domestication; +1 infant per litter). In support of our prediction, the results of the post hoc tests (*SI Appendix, Table S4*) indicate that the increase in total litter mass at birth observed in correlation with allonursing ( $P = 0.1$ ) is not driven by an increase in neonatal mass. Contrary to our prediction, no form of allocare, no matter how reliable, is associated with larger infants.

**Prediction 4:** Allonursing will have the strongest effect on reproductive power, while domestication will have the strongest effect on total lifetime reproductive output (as mass, not number of offspring). Prediction 4 is fully supported by our results: allonursing correlates with a 83.1% increase in mass produced per year, while domestication correlates with a 68.2% increase (Fig. 3); domestication ( $P < 0.0001$ ) but not allonursing ( $P = 0.108$ ) correlates with an increase (93.7%) in total lifetime reproductive output. Post hoc testing (*SI Appendix, Table S4*) indicates that this increase is at least partially driven by an increase in reproductive lifespan; however, the small effect size (+15.8%) suggests that other factors, such as higher fertility (effect size +96.2%), are likely greater contributors to the increase in lifetime reproductive output in domesticated taxa.

## Discussion

Domestication and different forms of alloparental care have different effects on female reproductive strategies (Fig. 4) without concomitant changes in either total energy expenditure (at least for alloparental care, while for domestication the results are tentative given the extremely small sample size) or basal metabolic rate. Our results suggest that total energy expenditure does not increase with allocare but that proportionally more energy is directed toward reproduction instead of other activities (e.g., locomotion, foraging, or defense), thus increasing reproductive output. Female reproductive output can be



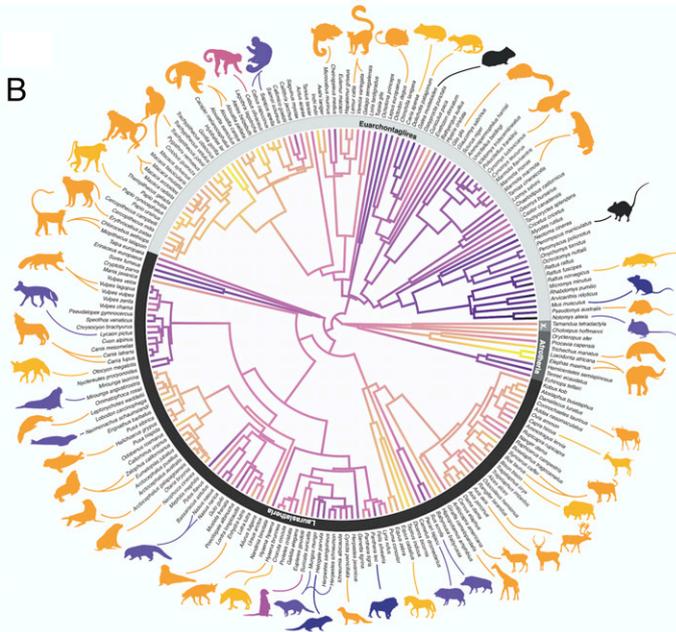
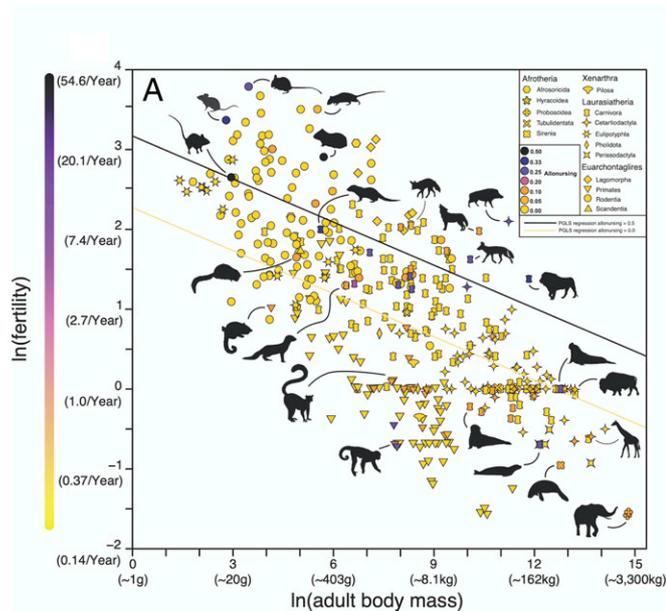
**Fig. 1.** (A) PGLS regressions describing the relationship between litter size and body mass in domesticated (blue) versus nondomesticated (pink) species. Domestication correlates with a significant increase in litter size. Silhouettes show a sample of domesticated taxa. (B) Phylogenetic tree of a subsample of species included in this study. Branch color indicates the mean litter size. Domesticated taxa are indicated.

improved by 1) altering the timing of reproductive events; 2) improving output at each reproductive event; and/or 3) increasing reproductive power.

**Infant Provisioning and Reproductive Output.** It has been proposed that the direct provisioning of human children allows earlier weaning (26). We find provisioning has a small, borderline-significant effect ( $P = 0.045$ , effect =  $-27.5\%$ ) on the age at

weaning, but our results indicate that a more-important driver of earlier age at weaning may be infant carrying, especially by males (although this model is not quite significant either:  $P = 0.0086$ , effect =  $-48.9\%$ ; male carrying is the model with the lowest AIC, and the AIC of “others carrying” is within 2).

Overall, however, we predicted that since infant provisioning occurs after the infant is weaned, the energetic input provided does not increase the energy available to the breeding female



**Fig. 2.** (A) PGLS regressions describing the relationship between fertility and body mass in species practicing allonursing (black, purple, and orange) versus species not practicing allonursing (yellow). Allonursing correlates with a significant increase in fertility. Taxa are coded by order (point shape) and degree of allonursing. Silhouettes show a subset of taxa that practice some degree of allonursing. (B) Phylogenetic tree of a sample of species included in this study. Branch color indicates fertility, and color of the species' silhouette expresses the proportion of nursing performed by nonmothers (black being 0.5, which is the highest value and means that an offspring receives an equal amount of milk from the mother and the allomother[s]).

**Table 1. Models in which either domestication or allonursing correlate with a significant difference in a measure of reproductive outputBest**

Response variable	Predicted by (Adult mass+)	P	n	Adjusted intercept difference*	Effect size (%)	Best AIC?†
Fertility (offspring/y)	Others provisioning	0.00124	411	0.42	52.5	Best
	Domesticated	0.0000002	936	0.46	58.9	No
	Allonursing	0.0042	411	0.45	56.5	No
	Combined carrying	0.0057	411	0.64	90.7	No
	Carrying by alloparents	0.0053	411	0.68	97.7	No
IBIs	Combined carrying	0.0018	313	-0.59	-44.6	Best
Lifetime reproductive output (neonatal litter mass)_K	Domesticated	0.0000002	431	0.66	93.7	Tied
Litter size	Domesticated	0.0000011	1,404	1.02	-	Tied
	Others provisioning	0.00045	425	1.12	-	Tied
	Allonursing	0.00072	425	1.29	-	Tied
Mass produced/y_K	Allonursing	0.00078	293	0.61	83.1	Best
	Domesticated	0.00000043	505	0.52	68.2	No
Neonatal litter mass_K	Allonursing	0.0000158	374	0.56	74.8	Best
	All provisioning + allonursing	0.00081	374	0.53	71.5	No
	Domesticated	0.0000096	921	0.34	39.9	No

\*Intercept difference is scaled so that the maximum value that each variable can take is 1 (e.g., for Allonursing, the maximum value is 0.5 [one-half of nursing is done by nonmothers], so the intercept difference is multiplied by 0.5 and then unlogged to be expressed as percentage). This makes the effect size for each variable directly comparable to each other.

†“Best” indicates that the model has the lowest AIC for that response variable, and no other model is within 2; “Tied” indicates that the model either has the lowest AIC but there are others within 2, or that its AIC is within 2 of the lowest; “No” indicates that the AIC score is >2 from the lowest AIC score for that response variable.

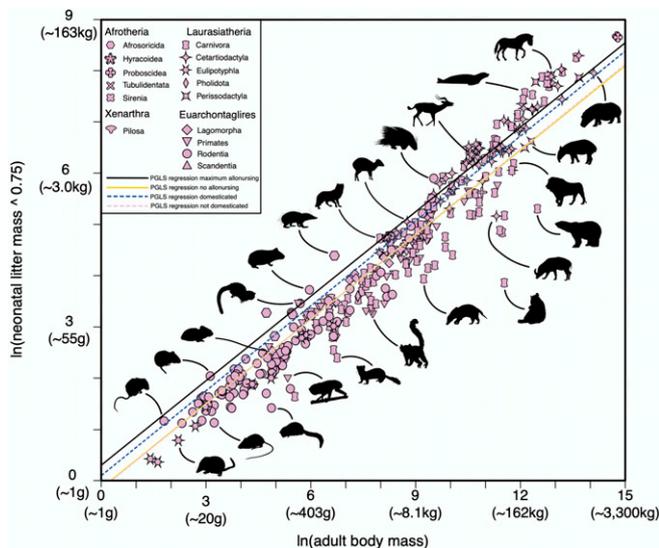
and would therefore have minimal impact on reproductive output (Prediction 1). Contrary to our prediction, our results indicate that provisioning by alloparents is the best model to explain variation in fertility (based on AIC). The effect of provisioning on fertility is not as large as those we observe for other forms of allonursing, especially infant carrying, however. Provisioning by alloparents also correlates with an increase in litter size, which likely contributes to the observed increase in fertility. We also find tentative evidence that this increase in litter size drives a possible increase in the total mass of the litter at birth ( $0.05 < P < 0.00625$ ). Infant provisioning by alloparents does not correlate with a change in mass of individual neonates,

suggesting that this change is driven entirely by an increase in the number of offspring. This result supports previous work (24) suggesting that in the presence of nonreliable external energetic supplementation, a species responds by adjusting its litter size rather than producing more expensive (larger brained) offspring. That energetic supplementation by alloparents affects litter size rather than neonatal mass may be explained by extrinsic mortality driving the trade-off between quality and quantity of offspring (27): in the event of infant death, the cost to the mother is higher for a larger offspring than for a smaller one (28).

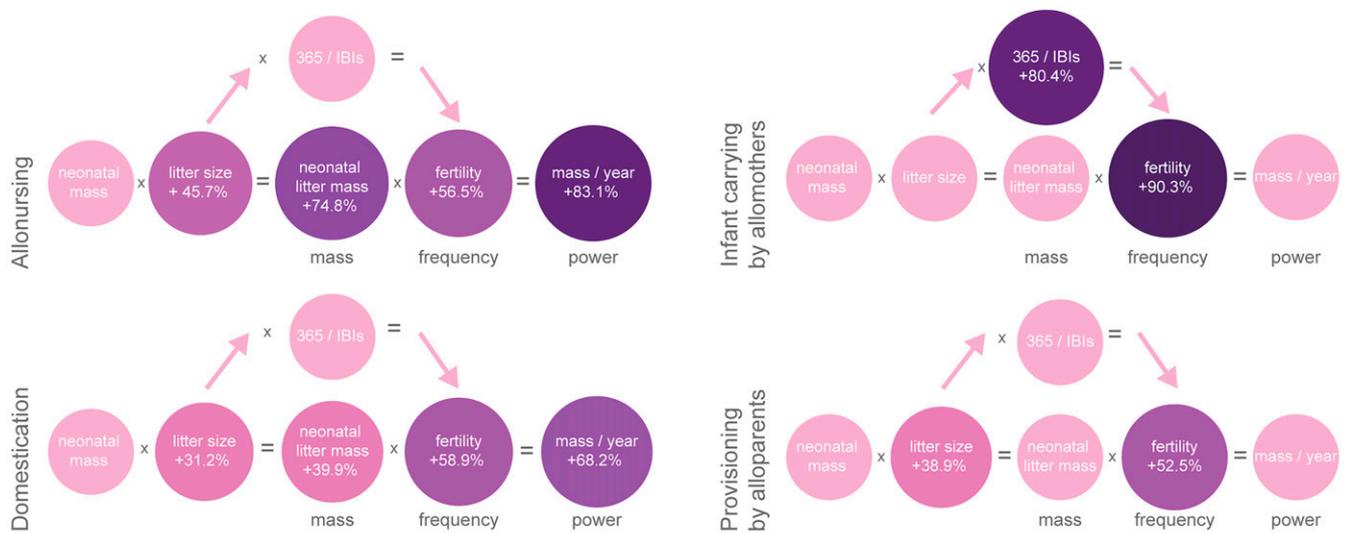
Additionally, the phylogenetic signal of litter size ( $K = 0.14$ ) is among the smallest we observe, while that of neonatal mass ( $K = 2.11$ ) is the highest. This indicates that litter size is substantially more evolutionarily labile than neonatal mass and will respond more quickly to an increase in energy availability. An animal’s mass is intimately related to the ways that it can interact with its environment and is closely linked to metabolism, brain size, diet, locomotion, and many other aspects of an organism’s anatomy, physiology, and behavior (29). This is especially true for newborns, for which mortality is highest and therefore tolerance for changes in the equilibrium between organism and environment is the lowest (30). Thus, other factors, unrelated to energy availability or extrinsic mortality, are likely acting to constrain the ability of taxa to respond to increased energy availability by producing larger offspring.

**Reproductive Timing and Increased Lifetime Reproductive Output.**

Previous research indicates that in domesticated species, age at first birth (22, 31) and IBIs (17, 32) are reduced (Prediction 2). This is a consequence of energetic supplementation leading to a higher growth rate as well as a decoupling of reproductive events from environmental seasonality. Since our dataset includes neonatal and adult mass but not age at which adult mass is achieved, we do not test directly whether growth rate (mass acquired per unit of time) is accelerated. However, by testing whether age at weaning is significantly different in species that are domesticated or practice allonursing, we are indirectly assessing whether the physiological traits required to process



**Fig. 3.** PGLS regressions expressing the relationship between neonatal litter mass and adult body mass in domesticated (blue, dashed) species and in those practicing allonursing (black, solid) versus nondomesticated (pink, dashed) and not practicing allonursing (yellow, solid). Allonursing has a stronger effect than domestication.



**Figure legend:**

circle area is proportional to the percent increase; circle color is divided in 8 categories, from no significant increase to 100% increase



**Fig. 4.** Graphic describing the proportional change in the several types of response variables in association with either domestication of different forms of allomaternal care. Adjusted values (according to Kleiber's Law) are taken for the models having either neonatal litter mass or derived variables.

and digest food, and the sensory-motor ones necessary to acquire it, are attained at an earlier age. Hence, an earlier age at weaning would be indicative of a faster growth, at least from a physiological point of view. We do not find evidence of an earlier age at weaning in domesticated taxa. In line with previous research on primates (33), we find tentative evidence ( $0.00625 < P < 0.05$ ) for infant carrying and provisioning, by either males or alloparents, to reduce age at weaning (*SI Appendix, Table S3*).

We would also expect that a longer reproductive lifespan induced by an earlier age at first birth and an increased reproductive frequency should result in an increased lifetime reproductive output (22). To measure reproductive output while accounting for trade-offs between offspring quantity and quality, we use the compound variable neonatal litter mass, calculated as litter size multiplied by adjusted neonatal mass. To assess lifetime reproductive output, we measured lifetime neonatal mass as reproductive years divided by IBIs multiplied by adjusted neonatal litter mass. Our results confirm our prediction (Prediction 2) by showing that lifetime reproductive output is higher (+93.7%;  $P < 0.0001$ ) in domesticated species. However, conversely to what is expected, neither age at first birth nor IBIs are significantly reduced in domesticated species when imposing our conservative alpha level. This latter finding suggests that increased lifetime reproductive output (which is measured as mass produced over a lifetime) is predominantly driven by an increase in the mass of each litter rather than in the frequency of births. Domesticated species produce more offspring per litter, without reducing their birth weight, than nondomesticated species.

We found that IBIs are significantly reduced in species where both paternal and alloparental infant carrying is present but not each individually. This suggests that these “babysitters” promote the evolution of a maternal organism that is capable

of successfully acquiring the same amount of energy in a shorter period, since we find no evidence of a decrease in litter mass accompanying an increase in IBIs. This is consistent with previous findings suggesting a relationship between reproductive timing and allomaternal care in primates (8, 33, 34).

**Energy Availability Limits Reproductive Output.** The limiting effects of energy availability on reproductive output are both well established (35, 36) and intuitive, with recent research (37) highlighting the alternative strategies that females can undertake to cope with the energetic constraints on reproduction, such as getting help from alloparents or storing energy in the form of body fat. Accordingly, we find that all forms of energetic supplementation occurring before weaning (domestication and allonursing) correlate with an increase in neonatal litter mass and in reproductive power (as per Prediction 3). We do not find evidence for a reallocation of maternal energy expenditures due to babysitting and/or communal nesting and/or infant protection having any effect on reproductive output in terms of litter size or mass. This suggests that the benefits of this type of allocare might be either in the form of a trade-off in favor of metabolically expensive tissues [e.g., brain mass (16)] or provide other negligible benefits to the mother but important ones to the alloparent [reviewed by Riedman (38)]. Both provisioning by alloparents and infant carrying by allomothers correlate with an increase in fertility, which in the former case is likely driven by litter size and in the latter by IBIs. Essentially, both forms of allocare allow for an increase in reproductive frequency, but they seem to do so by lifting different constraints: help in taking care of offspring reduces the time between reproductive events (as per Prediction 3), while provisioning of the offspring, even postweaning, increases the size of the litter (unlike predicted).

**Maternal Metabolism Limits Reproductive Power.** The most striking results of our study are that it is not the amount of energy available as food that most benefits a breeding female. Arguably, the energetic supplementation to domesticated mothers is virtually unlimited since domesticators aim to maximize the reproductive output of animals. One would therefore expect that the effect of domestication on reproductive output would be larger than that of allonursing. This is not the case: compared to domestication, allonursing has a slightly stronger effect on litter size, double the effect on neonatal litter mass (both measured as raw value or adjusted according to Kleiber's law) and a ~20% stronger effect on mass produced per year (as per Prediction 4). Allonursing is a unique form of energetic supplementation in that it acts independently from the maternal metabolism. This decoupling of energetic supplementation from the maternal metabolism occurs at the time when energetic supplementation is most needed: lactation is costlier than gestation (36). Thus, it may be that allonursing, uniquely among other forms of allocare and external energetic supplementation, can increase reproductive output with some degree of independence from maternal mass.

Previous research, recently reviewed by Pontzer (39), has found that an organism's physiological limits on energy expenditure are capped (40) regardless of energetic supplementation (41). Sustained energy expenditure is related to basal metabolism (42–44). Specifically, in humans, an increment of expenditure above 2.5× basal metabolic rate (BMR) cannot be sustained by increased energetic intake, therefore posing a metabolic limit to its duration. Similarly, experimental work on nursing mice has shown that energy throughput is limited (45). Gestation, and more so lactation, are among the most metabolically expensive activities an adult mammal undertakes (36). Recent work (41) has shown that at least in humans, reproduction approaches the limit of sustained expenditure (~2.2× BMR). This is supported by evidence of maternal depletion in humans in the case of early (during which the body is still investing energy toward growth) or frequent reproductive events even in industrialized societies when there is virtually no limit on energetic intake (46). It is also supported by recent research showing that postpartum (lactational) amenorrhea decreases in duration in industrialized societies (47). Consequently, we argue that the increase in litter mass and in mass produced per year observed in domesticated species (+39.9% and +68.2%, respectively, compared to nondomesticated relatives) may represent the reproductive limit imposed by the sustained energy expenditure of the organism. Additionally, we argue that allonursing releases this limit on sustained energy expenditure, allowing for a substantial increase in neonatal litter mass and mass produced per year (+74.8% and +83.1%; Fig. 4).

The theories attempting to explain the evolution of the costly and seemingly altruistic behavior of allonursing are reviewed and critically assessed by MacLeod and Lukas (48). They found that the likelihood of allonursing evolving is more related to its costliness than to its benefit to the allonurse. Species with larger litters have a lower nursing cost per infant and a higher probability of infant mortality, making mothers more frequently available to nurse others' infants with a relatively low cost (13). Allonursing appears to function as a type of ante litteram sharing economy of milk. Based on our results, we suggest that reproductive power is optimized, both at the species level and on an individual level over the long term, when the practice of allonursing allows all breeding females to lactate at their maximum metabolic capacity, even in the instances in which some of their offspring die as a consequence of extrinsic mortality (e.g., predation) and their milk production would otherwise decrease (49, 50). On one hand, milk is an extremely expensive but highly perishable (nonstorable) good, which can provide a benefit only if there are infants ready to suckle it. On the other hand, the high metabolic demand placed on a lactating female

limits her ability to increase her reproductive output even in the case of limitless energetic resources, as determined by the power of her metabolism. We therefore propose that this particular type of allocare, allonursing, is capable of lifting the metabolic constraint on maternal reproductive power (energy transformed per unit of time) while optimizing the distribution of milk between breeding females in species with high and unpredictable infant mortality. As a result, the energetic burden is more evenly distributed across all mothers (37) regardless of fluctuations in infant mortality or the genetic relatedness between infant and nurse. As with all volatile economies, flexibility in resource allocation and ability to rapidly reinvest (in another female's offspring, presumably with the expectation of reciprocity) are key to resource optimization (51). Future work assessing the correlation between extrinsic mortality and prevalence of allonursing as well as the degree of long-term reciprocity in allonursing within a population would greatly inform the interpretation of our results.

## Materials and Methods

**Data Collection.** Data for this study were compiled from several ( $n = 40$ ) published sources. We collected continuous measures of allomaternal (paternal and alloparental) care for placental mammals from Isler and van Schaik (16). The variables collected measured the frequency of occurrence of different allomaternal care behaviors, either by the male (usually, the breeding male in pair-living species but, rarely, any adult male in polygynous or multimale, multifemale groups) or by nonparent group members (16) (alloparental care). These care behaviors included provisioning of the infant and/or of the mother, carrying, protection, allonursing, and a variable (communal work) that comprised other energetically influential care behaviors (e.g., pup retrieval). Hence, these measures only reflect direct allomothering, and do not include the indirect benefits to infants such as troop defense. We derived additional variables expressing allocare by summing the frequencies of the primary ones. These additional variables express the type of allocare (nutritional supplementation or help in infant care) regardless of who is performing it (*SI Appendix, Table S1*) (e.g., for *Mus musculus*: Combined carrying = 0 for male carrying + 0 for alloparental carrying + 0.33 for communal work; energy in = 0.33 for allonursing + 0 for male provisioning + 0 for provisioning by others + 0 for provisioning of mothers).

In addition to this allocare data, we collected data for adult mass [female mass if available, otherwise pooled between males and females (24)], neonatal mass, age at weaning, age at first birth, IBIs, litter size, litter per year, maximum lifespan, metabolic rate, and TEE from several published sources (16, 24, 48, 52–58). When data for the same species were reported by more than one source, the arithmetic mean was used in the analysis. Additionally, from these values we derived the following variables: neonatal litter mass as neonatal mass multiplied by litter size; reproductive years as maximum lifespan minus age at first birth; lifetime neonatal mass as reproductive years divided by IBIs multiplied by neonatal litter mass; annual fertility as litter size multiplied by litters per year; and mass produced per year as neonatal litter mass multiplied by annual fertility (*SI Appendix, Table S1*). Our neonatal litter mass variable is an attempt to standardize for the tradeoffs between litter quantity and quality. The energy requirements of organisms do not scale linearly with body mass, however, so we ran all our models that include neonatal litter mass in both their raw form and in an alternate form. In the alternate form, following Kleiber's law, neonatal mass was elevated to the 0.75 power before being multiplied by litter size. In the manuscript, figures, Table 1, and *SI Appendix, Table S3*, we report the results of the models using the adjusted values, while in *Dataset S4* we report both sets of models and results. All dimensional values were converted to grams for mass and to days for time. We supplemented our dataset with other sources in the instances of missing data for domesticated species (59–89). Given the extensive size variation present in some domesticated species, we made sure to select all variables from the same breed (e.g., German shepherds for dogs) of approximately similar size to wild counterparts under normally reproducing conditions. All data used in the analyses presented in this manuscript, together with their references, are provided in the *SI Appendix*.

The total sample includes 1,806 species, representing almost all domesticated mammals ( $n = 20$ ) and 445 species with allocare data across all placental orders: Afrosoricida (0.8%), Carnivora (12.6%), Cetartiodactyla (13.7%), Chiroptera (7.3%), Cingulata (0.8%), Dermoptera (0.1%), Eulipotyphla (4.5%), Hyracoidea (0.2%), Lagomorpha (2.5%), Macroscelidea (0.6%), Perissodactyla

(0.9%), Pholidota (0.4%), Pilosa (0.4%), Primates (13.4%), Proboscidea (0.1%), Rodentia (40.7%), Scandentia (0.3%), Sirenia (0.3%), and Tubulidentata (0.1%).

**Data Analysis.** We assessed the effects of *allocare* and domestication on life history variables using phylogenetic generalized least squares (PGLS) regressions (90). Our PGLS regressions used the species-level mammal phylogeny from Upham and colleagues (91). We used their maximum clade credibility tree calibrated using node dates and an exponential prior. To this published tree, we added *Canis familiaris* diverging from *Canis lupus* at 15,000 y ago (92). Adult body mass was included as a covariate in all analyses. We used the additive effects of each independent variable (*allocare* or domestication) to estimate effect size and tested for significant differences between intercepts using a Student's *t* test. To compare effect sizes across different explanatory variables, we scaled the intercept difference so that the effect size reflects the maximum value that the variable can take (e.g., for allonursing, the maximum value is 0.5 [one-half of nursing is done by nonmothers]), so the intercept difference is multiplied by 0.5 and then the difference in the natural log of the effect sizes is exponentiated to convert back to the original ratio of the effect sizes (which we then express as a percentage increase).

All variables related to mass or time were logged to account for the high degree of skew in these variables across placental mammals. Following published literature (16, 52, 57), we did not log data for litter size, number of litters per year, or the various *allocare* variables. All statistical analyses were performed using R version 4.0.1 (93). We estimated  $\lambda$  for the PGLS models independently for each regression using maximum likelihood. PGLS analyses were conducted using the "pgls" function in the R package "caper" (94). To account for multiple hypothesis testing, we adjusted our alpha level to account for each independent explanatory variable: domestication, others provisioning, male provisioning, allonursing, communal work, male carrying, and alloparental carrying. Additional explanatory variables used in this analysis are combinations of these primary eight (SI Appendix, Table S1). Thus, we use an alpha level of 0.00625 (0.05/8) to identify statistical significance for phylogenetic ANOVAs. To control for the possible constraining effect of seasonality on IBIs, we ran all the models with IBIs as response variable both on the full dataset and on a reduced dataset that excluded species with IBIs of exactly 1 y (365 d).

To further compare the explanatory power of the several models having the same response variable, we used the AIC (95). Using AIC required a reduction of the original sample for the domestication models to ensure all models compared had the same sample size (the reduced domestication models with all the parameters and results are in Dataset S6).

Each prediction postulates specific effects in specific models (also see SI Appendix, Fig. S1 for a general overview):

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