Revisiting non-offspring nursing: allonursing evolves when the costs are low

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Allonursing, the nursing of another female's offspring, is commonly assumed to have evolved through the benefits of kin selection or reciprocity. The evolution of allonursing may also be influenced by variation in the possible costs to allonurses. The relative influence of costs and benefits on the incidence of allonursing in mammals remains unexplored. We show, using comparative analyses, that where females group with kin, the presence or absence of allonursing is not associated with variation in relatedness or relative offspring altriciality. Allonursing is most common where females produce litters. In cooperative breeders, where litter-bearing is ubiquitous, carnivores are most likely to allonurse. Our results suggest that variation in the potential benefits is not associated with the distribution of allonursing, but that allonursing can quickly evolve when the costs to allonurses of nursing additional offspring are low.
Introduction

Allonursing, the nursing of non-descendant infants, occurs in a wide variety of mammals where females live in groups, including primates, cetaceans, and canids [1]. Allonursing may confer substantial benefits to offspring in terms of growth, survival, and the transfer of immune compounds [2, 3]. These benefits come at a cost to the allonurse, as lactation is highly energetically demanding [4]. Several hypotheses have been suggested to explain the evolution of this costly behaviour, most focusing on potential adaptive benefits to be derived from allonursing: females may nurse to gain experience of maternal care; nursing may be a means of evacuating excess milk which may be painful, or impede mobility; nursing may increase the likelihood of reciprocity; or, nursing may provide indirect benefits where females are able to preferentially nurse related offspring [5, 6].

Contrasts in the relative frequency of allonursing across taxonomic groups are also likely to reflect variation in the costs of nursing. For example, Packer et al. [1] showed that in wild mammals, non-offspring nursing is most common in species where females produce multiple offspring in litters (polytocous) relative to where females produce single offspring (monotocous). Where females produce litters, the investment per offspring is lower and an increase in litter size does not result in a linear increase in total effort [7]. Producing milk for an additional offspring is therefore unlikely to be highly costly in polytocous species, and as a result, allonursing may have been able to evolve in these species.
Here, we extend the work of Packer et al. [1] by reanalysing the ecological correlates of non-offspring nursing, including a number of previously untested variables, in line with a new question: has non-offspring nursing evolved only where it is likely to generate substantial fitness benefits, or has it been more constrained by costs? Where females are related, indirect benefits are guaranteed - but variation in the magnitude of probable returns exist. If the evolution of allonursing is driven by variation in potential benefits, it should be most common where the benefits are likely to be highest: where offspring are highly altricial, or where individuals are closely related (in cooperative breeders, and where groups are small) [8, 9]. If allonursing is constrained by cost, it should occur where costs are likely to be lowest: where resources are plentiful; if milk is relatively cheap to produce; and where relative investment per offspring is low (multiple offspring produced per breeding attempt, a number of breeding attempts a year). Allonursing might also be influenced by opportunism costs, and may therefore be more likely to occur when several females breed concurrently in close proximity over a short breeding season [5].

Methods

Using the criteria of social system classification specified by Lukas & Clutton-Brock [9], we defined 120 mammalian species as group-living. Thirty four of these were classed as cooperative breeders (one female is the primary breeder, subordinate individuals help to rear her offspring) [10]. We classed species as allonursing if females regularly allonurse in wild populations. A lack of evidence of allonursing was taken as evidence of its absence only where sufficient behavioural studies exist. We expect this protocol to be sufficiently rigorous
as allonursing is an easily observed behaviour, and likely to be reported. To ensure that we
did not incorrectly classify a species because of insufficient study, we excluded species for
which insufficient behavioural or wild data were available (N = 12, indicated in datafile).

We compiled data on mean litter size, number of litters produced per year, and group
size; milk composition (sum of percentage protein, fat, and sugars); and diet. We defined
species as seasonal breeders if breeding is restricted to a period of six months or less. We
used two measures of relative altriciality: residuals of a phylogenetic regression of neonate
and adult body mass, which corrects the differences between species according to shared
phylogenetic; and the standard residuals of a log-log regression of neonate and adult body
mass. Both use data on 925 mammalian species [11]. The first measures altriciality relative
to species in the same phylogenetic group; the second measures altriciality relative to all
mammals. All continuous variables were log-transformed before analyses. Data and
references are provided in the supplementary material.

A model was constructed to test the effect of group structure (whether species breed
cooperatively, or not) on allonursing incidence using the package “MCMCglmm” [12],
specifying whether allonursing occurs or not as a binary dependent variable. The updated
mammalian supertree [13] was used as the basis for phylogenetic analyses. We ran this
model with and without the phylogenetic tree specified, and compared models using DIC
[14]. Including phylogeny did not improve model fit, suggesting that phylogenetic similarity
does not explain residual variance. We did not account for phylogeny in subsequent models.
We split the data into cooperative and non-cooperative breeders, and in each subset constructed preliminary models using the lme4 package in R [15] to look at factors that might influence: (i) costs that might prevent females from allonursing (diet, litters produced per year, mono/polytocy); (ii) the probability that other females in the group will have offspring (litters produced per year, group size, breeding season); and (iii) the potential benefits of allonursing or receiving milk (relative altriciality, group size). As all cooperative species were polytocos, we used litter size instead of mono/polytocy in analyses of cooperative species. We tested the effect of milk composition on allonursing incidence in separate models due to low sample size. Where there was collinearity between variables, the variable that explained most variation (tested using AIC comparison of single-parameter models) was included and the other discarded. Global models were then defined for each subset by taking any significant variables in the preliminary models, and setting them as explanatory variables in a global model.

Results

Proportionally fewer cooperatively breeding species allonurse (29%, \( N = 24 \)) than non-cooperative group-living species (45%, \( N = 83 \)). This difference was not statistically significant (MCMCglmm \( P = 0.13 \)). Milk composition was not an important predictor of
allonursing in cooperative species (GLMM $Z_f = 1.17, P = 0.13$) or non-cooperatively breeding species (GLMM $Z_{23} = 1.13, P = 0.23$).

In cooperative breeders, carnivorous species were significantly more likely allonurse than omnivorous species (Table 1.a). No herbivorous cooperative breeders allonursed. Preliminary models also suggested a positive correlation with litter size (model i), and altriciality (model ii): these variables correlated significantly with diet, which was a better predictor of allonursing according to AIC in both cases. Allonursing was more common in larger groups (models ii and iii), but this effect was not significant.

In non-cooperatively breeding species, polytocos species were more likely to allonurse than those producing single offspring (Table 1.b). Preliminary models also suggested a negative correlation with group size (model iii). Group size and mono/polytocy correlated significantly, and mono/polytocy was a better predictor of allonursing according to AIC.

Discussion

In species where helping behaviour between females is likely to lead to indirect fitness benefits, the evolution of allonursing appears to be constrained by costs rather than being explained by differences in the likely returns. Polytocy positively affected allolactation incidence in non-cooperatively breeding species, in agreement with the results of Packer et
al. which suggest that non-offspring nursing in monotocous species, where investment per offspring is high and diverting care to other young is likely to be prohibitively costly, is best understood as milk theft [1]. Our results suggest that allonursing can quickly evolve when relative investment per additional offspring is low [6].

Allonursing was not more common in cooperative breeders or small groups where relatedness is likely to be highest. Within-species studies show that females that nest in kin groups do not necessarily preferentially nurse close kin [16, 17], suggesting that where females are likely to be related to some degree, directing care towards close kin may provide limited extra benefits. Similarly, variation in relatedness may generate little variation in the potential benefits of allonursing between species, and may therefore be unlikely to drive differences in allonursing incidence.

In cooperative breeders, where relatedness is high irrespective of helper number, there was a non-significant correlation between allonursing incidence and group size. Availability of potential helpers may be a more important predictor of allonursing, and allonursing might therefore be more likely to occur in larger groups. In contrast, in non-cooperative species we show a trend towards higher allonursing incidence in smaller groups, though polytocy remained a better predictor. This trend is in line with the results of Packer et al. that showed that in polytocos species, allonursing is more common where group size is small [1]. Taken with our results, this suggests that decreases in group size might increase the likelihood of allonursing, but polytocy is an important constraint.
In cooperative species, allonursing was most common in carnivores, a pattern which also may be explained by lowered costs of caring for additional young during periods of high resource availability. Carnivorous diets are subject to temporal and spatial fluctuation in resource availability, and reproduction often coincides with periods of trophic abundance [18, 19]. If provisioning ceases to influence offspring growth after a certain limit, as in cheetahs [20], there may be little cost to diverting extra resources to other offspring when food is plentiful.

Our results show for the first time that allonursing incidence is also not associated with offspring altriciality, in contrast with the link between alloparental care and altriciality in birds [21]. Lactation may reduce the reliance of young on extra care [22], allowing altriciality to evolve without alloparental care. Alternatively, our assumption that altricial offspring are more energetically demanding to rear than precocial young (making the benefits of allonursing greater) may not hold true in all species. Primates produce precocial young but have exceptionally long lactation periods [23], and, in precocial caviomorphs, the overall energy demand of nursing is comparable to that in rodents which produce altricial young [24].

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Data accessibility

All data are available in the electronic supplementary material.

References


Table 1. Generalized linear models testing factors associated with costs, benefits, and the likelihood of other females also having offspring on the incidence of allolactation within a) cooperatively breeding species and b) non-cooperatively breeding species.

<table>
<thead>
<tr>
<th>Model</th>
<th>Term</th>
<th>Estimate</th>
<th>SE</th>
<th>Z</th>
<th>P</th>
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<tbody>
<tr>
<td>a) Cooperatively breeding species</td>
<td>Intercept</td>
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<td>6.67</td>
<td>-1.30</td>
<td>&lt;0.01</td>
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<td>i) COSTS</td>
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<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
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<td></td>
<td>Herbivore</td>
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<td>-1.33</td>
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<td></td>
<td>Omnivore</td>
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<td>ii) CONCURRENT OFFSPRING</td>
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<td></td>
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<td>Mono/polytocy</td>
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<td>0.49</td>
<td>3.29</td>
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</table>

*α* group size is modelled separately due to linear separation in this sample

*β* this model excludes herbivores as no herbivores allonurse in this sample, resulting in linear separation where they are included