

1 Revisiting non-offspring nursing: allonursing 2 evolves when the costs are low

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

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23 Introduction

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

35

36 Contrasts in the relative frequency of allonursing across taxonomic groups are also
37 likely to reflect variation in the costs of nursing. For example, Packer et al. [1] showed that in
38 wild mammals, non-offspring nursing is most common in species where females produce
39 multiple offspring in litters (polytocous) relative to where females produce single offspring
40 (monotocous). Where females produce litters, the investment per offspring is lower and an
41 increase in litter size does not result in a linear increase in total effort [7]. Producing milk for
42 an additional offspring is therefore unlikely to be highly costly in polytocous species, and as a
43 result, allonursing may have been able to evolve in these species.

44

45 Here, we extend the work of Packer et al. [1] by reanalysing the ecological correlates
46 of non-offspring nursing, including a number of previously untested variables, in line with a
47 new question: has non-offspring nursing evolved only where it is likely to generate
48 substantial fitness benefits, or has it been more constrained by costs? Where females are
49 related, indirect benefits are guaranteed – but variation in the magnitude of probable
50 returns exist. If the evolution of allonursing is driven by variation in potential benefits, it
51 should be most common where the benefits are likely to be highest: where offspring are
52 highly altricial, or where individuals are closely related (in cooperative breeders, and where
53 groups are small) [8, 9]. If allonursing is constrained by cost, it should occur where costs are
54 likely to be lowest: where resources are plentiful; if milk is relatively cheap to produce; and
55 where relative investment per offspring is low (multiple offspring produced per breeding
56 attempt, a number of breeding attempts a year). Allonursing might also be influenced by
57 opportunism costs, and may therefore be more likely to occur when several females breed
58 concurrently in close proximity over a short breeding season [5].

59

60 Methods

61

62 Using the criteria of social system classification specified by Lukas & Clutton-Brock [9], we
63 defined 120 mammalian species as group-living. Thirty four of these were classed as
64 cooperative breeders (one female is the primary breeder, subordinate individuals help to
65 rear her offspring) [10]. We classed species as allonursing if females regularly allonurse in
66 wild populations. A lack of evidence of allonursing was taken as evidence of its absence only
67 where sufficient behavioural studies exist. We expect this protocol to be sufficiently rigorous

68 as allonursing is an easily observed behaviour, and likely to be reported. To ensure that we
69 did not incorrectly classify a species because of insufficient study, we excluded species for
70 which insufficient behavioural or wild data were available (N = 12, indicated in datafile).

71

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

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83

84 A model was constructed to test the effect of group structure (whether species breed
85 cooperatively, or not) on allonursing incidence using the package “MCMCglmm” [12],
86 specifying whether allonursing occurs or not as a binary dependent variable. The updated
87 mammalian supertree [13] was used as the basis for phylogenetic analyses. We ran this
88 model with and without the phylogenetic tree specified, and compared models using DIC
89 [14]. Including phylogeny did not improve model fit, suggesting that phylogenetic similarity
90 does not explain residual variance. We did not account for phylogeny in subsequent models.

91

92 We split the data into cooperative and non-cooperative breeders, and in each subset
93 constructed preliminary models using the lme4 package in R [15] to look at factors that
94 might influence: (i) costs that might prevent females from allonursing (diet, litters produced
95 per year, mono/polytocy); (ii) the probability that other females in the group will have
96 offspring (litters produced per year, group size, breeding season); and (iii) the potential
97 benefits of allonursing or receiving milk (relative altriciality, group size). As all cooperative
98 species were polytocous, we used litter size instead of mono/polytocy in analyses of
99 cooperative species. We tested the effect of milk composition on allonursing incidence in
100 separate models due to low sample size. Where there was collinearity between variables,
101 the variable that explained most variation (tested using AIC comparison of single-parameter
102 models) was included and the other discarded. Global models were then defined for each
103 subset by taking any significant variables in the preliminary models, and setting them as
104 explanatory variables in a global model.

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107 Results

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109 Proportionally fewer cooperatively breeding species allonurse (29%, $N = 24$) than non-
110 cooperative group-living species (45%, $N = 83$). This difference was not statistically
111 significant (MCMCglmm $P = 0.13$). Milk composition was not an important predictor of

112 allonursing in cooperative species (GLMM $Z_7 = 1.17$, $P = 0.13$) or non-cooperatively breeding
113 species (GLMM $Z_{23} = 1.13$, $P = 0.23$).

114

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

121

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

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129 Discussion

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131 In species where helping behaviour between females is likely to lead to indirect fitness
132 benefits, the evolution of allonursing appears to be constrained by costs rather than being
133 explained by differences in the likely returns. Polytochy positively affected allolactation
134 incidence in non-cooperatively breeding species, in agreement with the results of Packer et

135 al. which suggest that non-offspring nursing in monotocous species, where investment per
136 offspring is high and diverting care to other young is likely to be prohibitively costly, is best
137 understood as milk theft [1]. Our results suggest that allonursing can quickly evolve when
138 relative investment per additional offspring is low [6].

139

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

147

148 In cooperative breeders, where relatedness is high irrespective of helper number,
149 there was a non-significant correlation between allonursing incidence and group size.
150 Availability of potential helpers may be a more important predictor of allonursing, and
151 allonursing might therefore be more likely to occur in larger groups. In contrast, in non-
152 cooperative species we show a trend towards higher allonursing incidence in smaller groups,
153 though polytoxy remained a better predictor. This trend is in line with the results of Packer
154 et al. that showed that in polytocous species, allonursing is more common where group size
155 is small [1]. Taken with our results, this suggests that decreases in group size might increase
156 the likelihood of allonursing, but polytoxy is an important constraint.

157

158 In cooperative species, allonursing was most common in carnivores, a pattern which
159 also may be explained by lowered costs of caring for additional young during periods of high
160 resource availability. Carnivorous diets are subject to temporal and spatial fluctuation in
161 resource availability, and reproduction often coincides with periods of trophic abundance
162 [18, 19]. If provisioning ceases to influence offspring growth after a certain limit, as in
163 cheetahs [20], there may be little cost to diverting extra resources to other offspring when
164 food is plentiful.

165

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

175

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180 Data accessibility

181 All data are available in the electronic supplementary material.

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

		Estimate	SE	Z	P
a) Cooperatively breeding species					
i) COSTS	<i>Intercept</i>	-8.64	6.67	-1.30	
predicted: diet + litter size (n=21)	Litter Size	7.75	5.19	1.49	<0.01
	Diet				<0.01
	Herbivore	-7.05	5.28	-1.33	
	Omnivore	-4.46	2.47	-1.81	
ii) CONCURRENT OFFSPRING	<i>Intercept</i>	-5.40	3.21	-1.68	
predicted: litters per year + group size (n=12)	Group size	2.65	1.72	1.54	0.07
iii) BENEFITS	<i>Intercept</i>	-4.25	2.27	-1.87	
predicted: altriciality (phylo residuals) + altriciality (standard residuals) (n=16)	Standard residuals	-5.35	2.92	-1.83	<0.01
predicted: group size (n=14) ^a	<i>Intercept</i>	-5.22	3.11	-1.67	
	Group size	2.36	1.61	1.47	0.09
GLOBAL MODEL	<i>Intercept</i>	1.10	0.82	1.35	
predicted: diet (n=20)^b	Diet	-3.50	1.33	-2.64	<0.01
	Omnivore				
b) Non-cooperatively breeding species					
i) COSTS	<i>Intercept</i>	-0.97	0.35	-2.74	
predicted: diet + mono/polytocy (n=70)	Mono/polytocy	1.66	0.52	3.17	<0.01
ii) CONCURRENT OFFSPRING	<i>Intercept</i>	-0.53	0.35	-1.50	
predicted: litters per year + group size (n=35)					
iii) BENEFITS	<i>Intercept</i>	1.96	1.32	1.48	
predicted: altriciality (phylo residuals) + group size (n=41)	Group size	-0.96	0.49	-1.95	<0.05
GLOBAL MODEL	<i>Intercept</i>	-0.93	0.33	-2.85	
predicted: mono/polytocy (n=79)	Mono/polytocy	1.62	0.49	3.29	<0.001

244 ^a group size is modelled separately due to linear separation in this sample

245 ^b this model excludes herbivores as no herbivores allonurse in this sample, resulting in linear
 246 separation where they are included

247