

# 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 further variation in relatedness. Allonursing is  
14 most common where females produce litters; here the relative investment per offspring is  
15 low, and the costs of nursing additional young are likely to be reduced. 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. 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), probably because in litters the milk provided to each offspring is a lower  
41 proportion of the total, reducing the cost of nursing additional young [1]. In addition, in  
42 litter-bearing species females may have an increased likelihood of having an excess of milk  
43 due to loss of offspring or producing a relatively small litter [7]. Comparative models show  
44 that across mammals, for a given mass, females produce the same amount of offspring mass  
45 regardless of litter size, suggesting that total reproductive investment per offspring might be

46 lower in polytocous species [8]. Producing milk for an additional offspring is therefore likely  
47 to be less costly in polytocous species, possibly allowing allonursing to evolve.

48

49 Here, we extend the work of Packer et al. [1] by analysing the ecological correlates of  
50 non-offspring nursing in line with a new question: has non-offspring nursing evolved only  
51 where it is likely to generate substantial fitness benefits, or has it been more constrained by  
52 costs? Where females are related, indirect benefits are guaranteed – but variation in the  
53 magnitude of probable returns exist. If the evolution of allonursing is driven by variation in  
54 potential benefits, it should be most common where the benefits are likely to be highest:  
55 where individuals are closely related. If allonursing is constrained by cost, it should occur  
56 where costs are likely to be lowest: where food resources are reliable and cheaply obtained;  
57 and where relative investment per offspring is likely to be low (multiple offspring produced  
58 per breeding attempt, several breeding attempts a year). Allonursing might also be  
59 influenced by opportunism costs, and may therefore be more likely to occur when several  
60 females breed concurrently in close proximity over a short breeding season [5], or by  
61 offspring development and ecology, which may be reflected in milk composition [9].  
62 Differences in group structure (for example, whether species breed cooperatively) may  
63 further influence the benefits and costs of allonursing.

64

65 **Methods**

66

67 Using the criteria of social system classification specified by Lukas & Clutton-Brock [10], we  
68 defined 119 wild mammalian species as group-living. Thirty four of these were classed as  
69 singular cooperative breeders [10]: one female is the primary breeder, subordinate  
70 individuals help to rear her offspring, and allonursing is commonly a result of  
71 pseudopregnancy [11] or failed subordinate pregnancies [12]. In non-cooperatively breeding  
72 group-living species ( $N=85$ ), on the other hand, allonurses also nurse their own young. We  
73 classed species as allonursing if females regularly allonurse in wild populations. A lack of  
74 evidence of allonursing was taken as evidence of its absence only where sufficient  
75 behavioural studies exist. We expect this protocol to be sufficiently rigorous as allonursing is  
76 likely to be reported, but we acknowledge a potential bias against species in which  
77 allonursing may not be easily observed, for example in small burrowing or nesting rodents.  
78 To ensure that we did not incorrectly classify a species because of insufficient study, we  
79 excluded species for which insufficient behavioural or wild data were available ( $N = 14$ ,  
80 indicated in datafile).

81

82 We compiled data on group structure (cooperative breeders, non-cooperative group-  
83 living species); mean litter size; number of litters produced per year; average relatedness  
84 within groups; milk composition (sum of percentage protein, fat, and sugars); and diet. We  
85 defined species as seasonal breeders if breeding is restricted to a period of six months or  
86 less. All continuous variables were log-transformed before analyses. Data and references are  
87 provided in the supplementary material.

88

89           A model was constructed to test the effect of group structure (whether species breed  
90 cooperatively, or not) on allonursing incidence using the package “MCMCglmm” [13],  
91 specifying whether allonursing occurs or not as a binary dependent variable. The updated  
92 mammalian supertree [14] was used as the basis for phylogenetic analyses. We ran this  
93 model with and without the phylogenetic tree specified, and compared models using DIC  
94 [15]. Including phylogeny did not improve model fit, suggesting that phylogenetic similarity  
95 does not explain residual variance. We did not account for phylogeny in subsequent models.

96

97           Singular cooperative breeders and group-living species that do not breed  
98 cooperatively differ in the likelihood that allonurses also nurse young of their own [10]; the  
99 costs and benefits of allonursing are consequently likely to differ between these groups. We  
100 therefore split the data into cooperative and non-cooperative breeders, and in each subset  
101 constructed preliminary models using the lme4 package in R [16] to look at factors that  
102 might influence: (i) costs that might prevent females from allonursing (diet, litters produced  
103 per year, mono/polytocy); (ii) the probability that other females in the group will have  
104 offspring (litters produced per year, number of adult females, breeding season); and (iii) the  
105 potential benefits of allonursing (average within-group relatedness). As all cooperative  
106 species were polytocus, we used litter size instead of mono/polytocy in analyses of  
107 cooperative species. We tested the effect of milk composition on allonursing incidence in  
108 separate models due to low sample size. Where there was collinearity between variables,  
109 the variable that explained most variation (tested using AIC comparison of single-parameter  
110 models) was included and the other discarded. Global models were then defined for each

111 subset by taking any significant variables in the preliminary models, and setting them as  
112 explanatory variables in a global model.

113

## 114 Results

115

116 Proportionally fewer cooperatively breeding species allonurse (29%,  $N = 24$ ) than non-  
117 cooperative group-living species (45%,  $N = 83$ ). This difference was not statistically  
118 significant (MCMCglmm  $P = 0.13$ ).

119

120 In cooperative breeders, carnivorous species were significantly more likely allonurse  
121 than omnivorous species (Table 1.a). No herbivorous cooperative breeders allonursed.  
122 Preliminary models also suggested a positive correlation with litter size (model i): litter size  
123 correlated significantly with diet, which was a better predictor of allonursing according to  
124 AIC. There was a non-significant trend for species with higher within-group relatedness to  
125 allonurse (model iii).

126

127 In non-cooperatively breeding species, polytocous species were more likely to  
128 allonurse than those producing single offspring (Table 1.b): allonursing has been recorded in  
129 66% (21/32) of litter-bearing group living species versus 31% of monotocous species (16/51).  
130 Preliminary models also suggested a positive correlation with litters produced per year  
131 (model ii). Litters per year and mono/polytocy correlated significantly, and mono/polytocy

132 was a better predictor of allonursing according to AIC. Variation in within-group relatedness  
133 is not related to the incidence of allonursing in group living species.

134

135 Milk composition was not an important predictor of allonursing in cooperative  
136 species (GLMM  $Z_7 = 1.17$ ,  $P = 0.13$ ) or non-cooperatively breeding species (GLMM  $Z_{23} = 1.13$ ,  
137  $P = 0.23$ ).

138

## 139 Discussion

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141 In species where helping behaviour between females is likely to lead to indirect fitness  
142 benefits, the evolution of allonursing appears to be constrained by costs rather than being  
143 explained by differences in the likely returns. Allonursing was very common in non-  
144 cooperatively breeding species that are polytocous, in agreement with the results of Packer  
145 et al. which suggest that non-offspring nursing in monotocous species, where investment  
146 per offspring is high and diverting care to other young is likely to be prohibitively costly, is  
147 best understood as milk theft [1]. Our results suggest that allonursing occurs in a wide range  
148 of species and can quickly evolve when relative investment per additional offspring is low  
149 [6]. A two-species study of social carnivores reached similar conclusions: lions are more  
150 likely to nurse non-offspring when they have excess milk and when the needs of their own  
151 young are reduced, possibly a low-cost by-product of communal defence against infanticide  
152 [7].

153

154 Allonursing was not more common in cooperative breeders, which had a higher  
155 mean within-group relatedness ( $\bar{x} \pm S.D$   $r = 0.42 \pm 0.09$ ) than non-cooperatively breeding  
156 species ( $r = 0.17 \pm 0.12$ ). Within these groups, allonursing incidence also did not correlate  
157 with relatedness. Within-species studies show that females that nest in kin groups do not  
158 necessarily preferentially nurse close kin [17, 18], suggesting that where females are likely to  
159 be related to some degree, directing care towards close kin may provide limited extra  
160 benefits. Similarly, variation in relatedness may generate little variation in the potential  
161 benefits of allonursing between species, and may therefore be unlikely to drive differences  
162 in allonursing incidence. However, data on relatedness within wild groups was not available  
163 for many species, notably the primates. Further study of patterns of relatedness in these  
164 groups may help to illuminate or confirm our results.

165

166 Among cooperative breeders, allonursing was most common in carnivores. In these  
167 species, reproduction may coincide with short periods of relative trophic abundance [19, 20]  
168 which could potentially reduce the costs of subordinate reproduction for dominant breeders  
169 [21]. Overall, however, the incidence of allonursing in cooperatively breeding species was  
170 surprisingly low. The mean number of adult females per group in this sample was low (1.93,  
171 range 1-5), suggesting that allonursing may feasibly be restricted by opportunity costs and  
172 may only occur in species where groups regularly have more than one female of breeding  
173 age. In addition, interspecific differences among cooperative breeders in the likelihood of  
174 successful subordinate female breeding could result in further variation in the presence of  
175 potential allonurses; low incidences of allonursing in cooperative breeders may represent  
176 physiological constraints rather than adaptive behavioural decisions.



177

178           Our findings indicate that reproductive cooperation occurs in many species where  
179 females live with kin, across taxonomic groups and ecological conditions. However, our  
180 results do not permit us to estimate the potential benefits that reproductive cooperation  
181 might confer to females, and more detailed studies are necessary to investigate the role that  
182 allonursing might have in the evolution of female sociality.

183

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187

## 188 Data accessibility

189 All data are available in the electronic supplementary material.

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

		Estimate	SE	Z	P
<b>a) Cooperatively breeding species</b>					
i) COSTS predicted: diet + litter size (n=20)	<i>Intercept</i>	-6.87	7.22	-0.95	
	Litter Size	6.36	5.56	1.14	0.07
	Diet				<0.01
	Herbivore	-21.49	4809.16	-0.004	
	Omnivore	-4.02	2.37	-1.70	
ii) CONCURRENT OFFSPRING predicted: litters per year + number of adult females (n=18)	<i>Intercept</i>	-0.45	0.48	-0.94	
iii) BENEFITS predicted: average relatedness (n=13)	<i>Intercept</i>	0.15	0.56	0.28	
<b>GLOBAL MODEL</b> predicted: diet (n=24)	<i>Intercept</i>	<b>1.10</b>	<b>0.82</b>	<b>1.35</b>	
	Diet				<b>&lt;0.01</b>
	Herbivore	<b>-19.66</b>	<b>3261.32</b>		
	Omnivore	<b>-3.50</b>	<b>1.33</b>		
<b>b) Non-cooperatively breeding species</b>					
i) COSTS	<i>Intercept</i>	-0.97	0.35	-2.74	

predicted: diet + mono/polytocy (n=69)	Mono/polytocy	1.61	0.53	3.01	<0.01
ii) CONCURRENT OFFSPRING predicted: litters per year + breeding seasonality (n=47)	<i>Intercept</i> Litters per year	-0.15 1.43	0.31 0.71	-0.48 2.03	<0.05
iii) BENEFITS predicted: average relatedness (n=31)	<i>Intercept</i>	0.60	0.38	1.59	
<b>GLOBAL MODEL</b> predicted: mono/polytocy (n=78)	<i>Intercept</i> <b>Mono/polytocy</b>	<b>-0.93</b> <b>1.58</b>	<b>0.33</b> <b>0.50</b>	<b>-2.85</b> <b>3.18</b>	<b>&lt;0.00</b> <b>1</b>

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