1**Title: Group structure, kinship, inbreeding risk and habitual female dispersal**

2**in plural-breeding mammals**

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13Inbreeding risk and female mammal dispersal

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24**Abstract**

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26   In most plural breeding mammals, female group members are matrilineal relatives but, in 27a small number of species, all adult females are immigrants who are seldom closely related to 28each other. Some explanations of contrasts in female philopatry suggest that these differences are 29a consequence of variation in resource distribution and feeding competition, while others argue 30that they reflect variation in the risk of close inbreeding to philopatric females. However, neither 31explanation has been tested against quantitative comparisons. Here, we use quantitative 32comparisons and phylogenetic reconstructions to show that contrasts in female philopatry in 33plural breeders are associated with the risk that a female's father is reproductively active in her 34group when she starts to breed, supporting the suggestion that habitual female dispersal has 35evolved to minimize the risk of inbreeding.

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42**Introduction**

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44   Among social mammals where stable social groups contain more than one breeding 45female (plural breeders) there are marked differences in kinship between female group members. 46In most species, female group members are philopatric, matrilineal relatives but, in a few species, 47they are typically unrelated immigrants from other groups (Wrangham, 1980; Pusey & Packer 481987; Clutton-Brock, 2009) as in many species of birds (Greenwood, 1980; Clarke *et al.,* 1997; 49Riehl, 2011). These contrasts in kin structure have important consequences for the evolution of 50social behaviour: in plural breeders where most females are close relatives, cooperative or 51affiliative interactions females are relatively common, while, where females are unrelated, they 52are rare (Sterck, 1997, Clutton-Brock, 2009).

53   Interspecific differences in the kinship structure of female groups are a consequence of 54contrasting patterns of female philopatry and dispersal (Lukas *et al.,* 2005). In many plural 55breeding mammals, most breeding females have either been born in the group where they breed 56or have formed a new group in company with other females from their natal group (who are 57commonly their sisters) and female immigration into established breeding groups rarely or never 58occurs. We refer to these species as habitually philopatric (HP) species to reflect the fact that a 59large proportion of breeding females have never left their natal group. In contrast, in a relatively 60small number of social mammals, as well as many plural-breeding birds, most females leave their 61natal groups as adolescents or young adults and join other breeding units and few (if any) females 62remain and breed in the group where they have been born. We refer to these species (which 63include all the three African great apes, several monkeys, all group living equids and a number of 64bats) as habitual dispersers (HD).

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65   Two main explanations for the evolution of habitual female dispersal in plural breeders

66have been suggested. One, originally outlined by Wrangham (1980) for primates, and later

67developed by other primatologists (van Schaik, 1989; Sterck *et al.,* 1997; Koenig, 2002; Isbell,

682004), links contrasts in female dispersal to variation in the distribution of resources, arguing that

69female dispersal occurs in species where the value of individual food items is low and contest

70competition within groups is relatively rare. Under these conditions (it is suggested) linear

71hierarchies and supportive coalitions may be unlikely to develop, the benefits of associating with

72kin may be low and females may commonly disperse to avoid scramble competition for

73resources. Although this explanation of contrasts in the frequency of dispersal and the structure of

74primate groups was initially widely accepted, recent reviews have stressed its shortcomings on

75several grounds (Janson & van Schaik, 2000; Koenig & Borries 2006; Thierry, 2008). Attempts

76to estimate and compare the relative intensity of resource competition in different species are

77fraught with difficulties and it is questionable whether competition for resources is less frequent

78or less intense among primates where females habitually disperse than among species where

79females are philopatric (Snaith and Chapman, 2007; Thierry, 2008). Moreover, it is questionable

80whether there is any association between female philopatry and diet quality or food distribution

81either across primate species or across other mammals (Clutton-Brock & Lukas, in press).

82   The second suggestion is that habitual female dispersal occurs where the risk of close

83inbreeding to females that remain in their natal group is relatively high because breeding tenure

84of individual males or of male kin groups commonly exceeds the age at which females are ready

85to breed, causing females to leave their natal group to locate unrelated partners (Pusey, 1987;

86Berger, 1989; Clutton-Brock, 1989). Close inbreeding has been shown to have high costs to the

87fitness of offspring in many animals that normally outbreed (Morton *et al.*, 1956; Pusey & Wolff,

881996; Charlesworth & Charlesworth, 1987; Keller & Waller, 2002; Ruf *et al.*, 2011) and

89philopatric females commonly avoid breeding with familiar males (Packer, 1978; Clutton-Brock,

902009). A review of data available in the late 1980's suggested that habitual female dispersal in

91plural breeding mammals is consistently associated with breeding tenures of males (or of male

92kin groups) that exceed the average age of a female at first breeding while habitual philopatry of

93females is commonly associated with male tenures shorter than the age at which females begin to

94breed (Clutton-Brock, 1989) but the sample of species for which adequate data were available

95was too small for quantitative analysis. In contrast, empirical studies show that there are several

96species where females commonly breed in their natal group but male tenure exceeds the age of

97females at first breeding (spotted hyenas: Honer *et al.*, 2007; capuchin monkeys: Perry *et al.*,

982008), though a potential explanation for these is dominant males cannot monopolize breeding

99access to resident females so that females are able to breed with males that are not close relatives.

100   In this paper, we use the more extensive data on female philopatry and male tenure in

101plural breeding mammals now available and modern comparative methods to determine whether

102there is any consistent association between habitual female dispersal and the relative length of

103breeding tenures of dominant males among contemporary species. Subsequently, we use

104phylogenetic reconstructions to determine whether evolutionary transitions from habitual female

105philopatry to habitual female dispersal are associated with the duration of male tenure. To assess

106the possibility that any interspecific association between habitual female dispersal and male

107tenure are a consequences of changes in other social parameters, our models test whether there is

108any association between the incidence of habitual female dispersal and philopatry and population

109density, home-range area, group size and group composition. Specifically, we test whether

110transitions to habitual female dispersal are restricted to species where either (i) the reconstructed

111ancestral condition was for male tenure to exceed female age at first breeding or (ii) changes in

112female dispersal are associated with changes in IR.

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Materials and Methods

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115 *Data and comparative analysis*

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117   We obtained information on female dispersal from Greenwood (1980) and Lawson-

118 Handley & Perrin (2007) and articles citing these reviews as listed on ISI Web of Science. We

119 excluded all species where females are solitary from our analysis as well as all singular breeders

120 (species where reproduction in each group is monopolized by a single breeding female and other

121 females are excluded or suppressed), since in these cases females are obliged to leave their natal

122 group to breed. Our dataset included only plural breeders (species living in stable groups which

123 normally include several breeding females). For the purpose of our analysis, we defined HP

124 species as those where most breeding females were born in the group where they first breed and

125 HD species as those where most breeding females are unrelated immigrants. It is important to

126 appreciate that in many HP species, where most successful breeders are natals, a substantial

127 proportion of recruits may disperse and attempt to form new breeding groups, though their

128 success rates are low. For example, in red howler monkeys 73% of females leave their natal

129 group (Pope, 1992), but almost all successful breeders are individuals that inherit a breeding

130 position in their natal group (Pope, 2000). Data on all variables that our analyses considered were

131 available for 47 different mammals, of which 18 were classified as HD and 29 as HP (see Figure

132 1).

133   We searched the Web of Science ISI for information on female age of first reproduction

134 and male tenure length, recording the median number of months a dominant male retained its

135 tenure. Species were classified as showing a high risk of inbreeding (IR) if male tenure length

136 exceeded female age at first breeding. Data on the number of females and males per group was

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137extracted for primates from Nunn *et al.* (2001), and for the remaining species from the papers

138reporting male tenure length or cited references. Data on body mass, home-range size and

139population density were drawn from the "Pantheria" dataset (Jones *et al.*, 2009). The full dataset

140with references is listed in the Supplement. All continuous variables were log-transformed prior

141to analyses.

142   We initially used Mann-Whitney tests to assess whether HP species differ significantly

143from HD species in the number of breeding females per group, population density, home range

144size, male tenure length, age of female at their first reproduction, or inbreeding risk. To

145investigate the distribution of evolutionary transitions from female philopatry to female dispersal

146and their correlates, we used the recently constructed mammalian supertree (Bininda-Emonds *et*

147*al.*, 2007). To assess the influence of continuous variables across the phylogenetic tree, we

148initially performed a regression with female settlement pattern as the dependent variable that

149included a covariance matrix reflecting the phylogenetic distance among the species to account

150for similarities due to common descent. The covariance matrix was constructed based on the

151dated branches of the supertree and performed using the function "pglmestlambda" of the

152package 'geiger' (Harmon *et al.*, 2008).

153   To obtain insights into potential temporal relationships between transitions in patterns of

154female dispersal and other variables, we performed ancestral-state reconstructions for the log-

155transformed continuous variables across the phylogenetic tree using the likelihood approach as

156implemented in the function "ace" of the package 'ape' (Paradis, 2004). In cases of ambivalence

157(as for instance for the tree bat species in our sample), we used the information from the extended

158dataset to reconstruct the most likely ancestral state for the clade, and classify the transitions

159accordingly (for the bats suggesting two transitions to female dispersal, rather than one transition

160to female dispersal and one to female philopatry). Standardized, weighted contrasts for log-

161transformed continuous variables across all nodes were obtained using the function "pic" in the

162package 'ape'. We compared absolute values of these contrasts between nodes with no change in

163female dispersal to those between nodes with a change, using Mann Whitney tests to assess

164whether changes in females settlement patterns are significantly associated with changes in the

165other parameters. All statistical tests were performed in R version 2.11.1 (R Development Core

166Team, 2010).

167 **Results**

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169 *Comparison of species with female philopatry and dispersal*

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171   Compared to plural breeders where females are habitually philopatric (HP, see above),

172 HD species, where females habitually disperse, differ significantly in male tenure length and

173 inbreeding risk (IR), but not in the number of females or males per group, age of first

174 reproduction, population density, home-range size or body mass (see Table 1). In a binomial

175 regression that combined all factors, only IR had a significant association with female dispersal

176 (Estimate for IR 7.14, z = 2.54, p=0.01; all other p > 0.25, see Supplementary Table 1 for full

177 model), and IR remained the only factor in all reduced models (see Supplementary Table 1). The

178 same result was found in a regression that included a covariance matrix to correct for

179 phylogenetic relationship: IR was the only significant factor (Estimate for IR 0.9, T = 6.3, p <

180 0.001; all other p > 0.13; see Supplementary Table 2 for full model). IR is also a better predictor

181 than a combination of male tenure length and female age at first reproduction, as species with

182 habitual female dispersal are not consistently different from species with female philopatry in

183 either trait directly (see Figure 1). In addition, our analysis shows that female dispersal is linked

184 to phylogeny since the maximum likelihood estimate for lambda (which measures the fit to the

185 phylogeny) is different from zero (larger than 0.9 in all models, see Supplementary Table 2).

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187 *Phylogenetic contrasts in female philopatry and dispersal*

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189   Since the previous analysis indicated that phylogenetic similarity explained parts of the

190 contrasts in female dispersal, we carried out a maximum parsimony reconstruction of the

191ancestral state for female dispersal which showed that five transitions from habitual female

192philopatry to habitual female dispersal and five transitions from HD to HP are needed to explain

193the distribution of female dispersal in our sample (Figure 2). The inbreeding risk (IR) changes at

194eight of these transitions, with male tenure exceeding a female's age at first reproduction at all

195transitions to HD, and male tenure changing to less than a female's age of first reproduction at

196three of the transitions to HP. The two exceptions are howler monkeys *Alouatta seniculus,* where

197inbreeding between fathers and their daughters has been observed (Pope, 1992), and capuchin

198monkeys *Cebus spp.*, where daughters mate with unrelated males present in the group (Muniz *et*

199*al.*, 2006*).* Only one of the six cases where IR evolved is it not associated to a transition to female

200dispersal (spotted hyena: *Crocuta crocuta*).

201   The risk of inbreeding at these transitions between HP and HD is mainly caused by an

202increase in male tenure length: on seven of the ten branches where a transition in dispersal

203occurred, male tenure length changed accordingly. However, the independent contrasts in male

204tenure length across these transitions do not differ significantly from the contrasts at the nodes

205without transitions (average of the 10 weighted contrasts at transitions in female dispersal: 0.006;

206average of the 36 weighted contrasts with no transition in female dispersal: 0.000; Mann Whitney

207W = 182, p = 0.97). Similarly, none of the independent contrasts for female or male group size,

208population density or home range size differ between nodes with a transition between HP and HD

209and nodes without transition (see Supplementary Table 2).

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211 Discussion

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213   The results of this study support the suggestion that the evolution of habitual female 214 dispersal in plural breeding mammals is associated with male breeding tenures that commonly 215 exceed the age of females at first breeding. Among contemporary species, those showing habitual 216 female dispersal are characterized by longer durations of male tenure relative to female age at 217 first reproduction than those where females are habitually philopatric (Figure 1). In addition, 218 phylogenetic reconstructions suggest that transitions from habitual female philopatry to habitual 219 female dispersal are associated with increases in relative male tenure and inbreeding risk

220   These results support the suggestion that, in plural-breeding mammals, habitual female 221 dispersal has evolved where males have unusually long tenure and the risk of inbreeding to 222 females that remained in their natal group would be high. The existence of some species where 223 females breed in their natal group although male breeding tenure exceeds female age at first 224 breeding does not necessarily contradict this suggestion for, in some species, dominant males are 225 unable to monopolize access to females and females avoid mating with close relatives (Clutton-226 Brock & Isvaran, 2006; Isvaran & Clutton-Brock, 2007; Cohas & Allaine, 2009; Soulsbury, 227 2010). For example, both in in spotted hyenas (Honer *et al.*, 2007) or capuchin monkeys (Perry *et* 228 *al.*, 2008), daughters sometimes reach maturity in groups when their fathers are still active, but 229 females avoid mating with close relatives by mating selectively with recent immigrants. 230 Similarly, in species where both sexes commonly remain in their natal group their entire lives, 231 such as killer whales, females mate with males from other social group when groups encounter 232 each other (Baird, 2000).

233   Our analyses provide no support for the suggestion that contrasts in female dispersal 234 patterns between HP and HD species are consistently associated with ecological contrasts. In

235particular, we found no evidence for an association between habitual female dispersal and

236population density, home range area or body mass. While the smaller number of females in

237species with habitual female dispersal could potentially indicate restrictions on group size due to

238higher levels of feeding competition, our analysis shows that these differences are not directly

239associated with changes in female dispersal. One potential link between group size and female

240dispersal could be that males are more likely to monopolize small groups of females for an

241extended period of time than large ones. However, our results should not be taken to suggest that

242ecological parameters play no role in stimulating female dispersal and, in species where some

243females breed in their natal group while others disperse to form new breeding groups there is

244extensive evidence that the abundance and distribution of resources and the intensity of

245reproductive competition within groups can affect the relative frequency of dispersal (Clobert *et*

246*al.*, 2008; Clutton-Brock & Lukas, in press).

247   Although habitual female dispersal is relatively rare in plural-breeding mammals, it is

248common in group living birds and a substantial number of reviews and theoretical papers have

249sought to explain this difference. The prevalence of female philopatry in mammals may be a

250consequence of polygynous mating systems, which commonly reduce the relative breeding tenure

251and longevity of males and so reduce IR and permit the evolution of female philopatry (Clutton-

252Brock & Isvaran, 2006; Clutton-Brock, 2009). In most birds that live in stable groups, females

253are capable of breeding by their second year of life while male breeding tenures often exceed two

254years (Ekman, 2004; Konig & Haydock, 2004). As a result, a possible explanation of contrasts in

255dispersal between group-living birds and mammals is that the chance that females which remain

256in their natal group will reach sexual maturity while their father is still the resident breeding male

257is usually higher in birds than mammals (Clutton-Brock, 2009). However, in most group living

258birds, a single female is responsible for a large proportion of successful breeding attempts

259(Raihani & Clutton-Brock, 2010) and an alternative or additional possibility is that female

260dispersal is more common in birds because high levels of reproductive skew among female birds

261stimulate more frequent dispersal by younger or more subordinate females.

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mean female age at first reproduction in females *(log months)*

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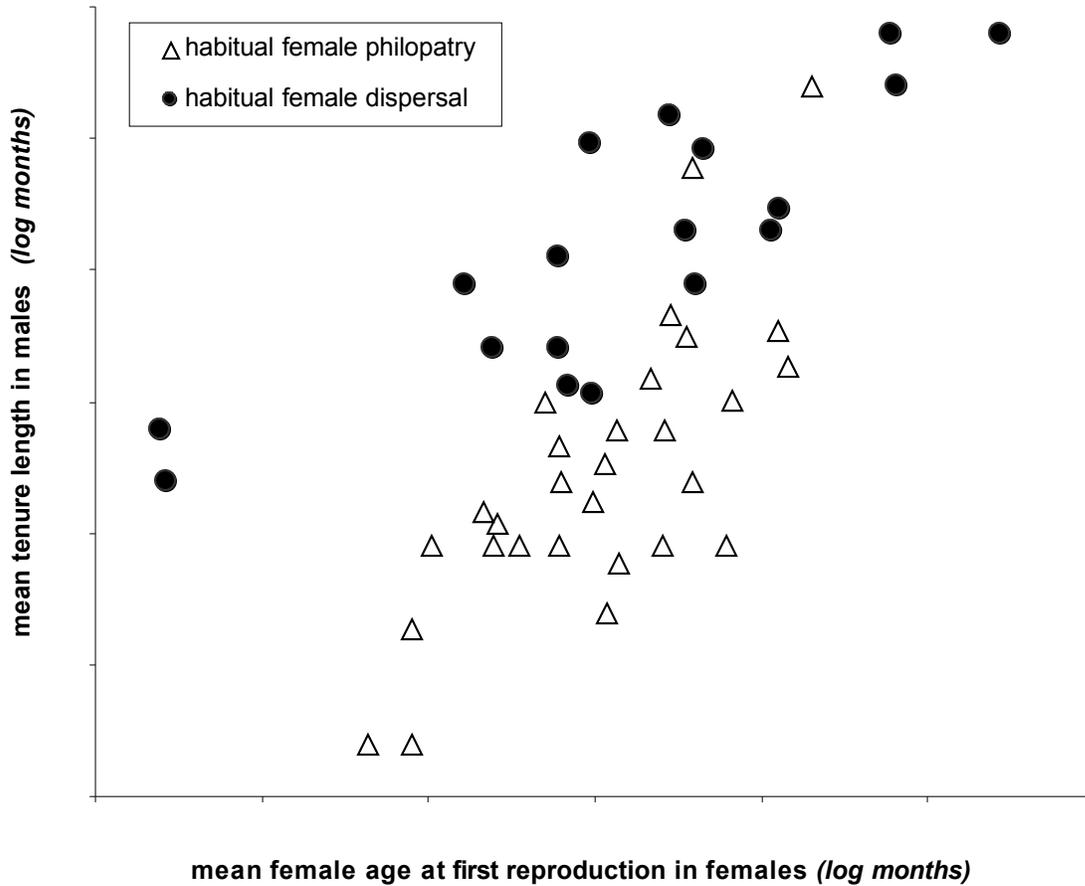
Figure 1: Relationship between mean tenure length in males and mean female age at first reproduction across plural breeding mammals

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Neither male tenure length nor female age at first reproduction differ consistently between HP and HD species. However, all HD species show values of male tenure length that exceed female age at first breeding while this is the case for only four HP species. Each dot represents the values for a single species.

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Macropus giganteus
Tamandua tetradactyla
Desmodus rotundus
Saccopteryx bilineata
Crocuta crocuta
Panthera leo
Meles meles
Equus caballus
Equus zebra
Equus burchellii
Cervus elaphus
Ovis canadensis
Lemur catta
Saimiri sciureus
Saimiri oerstedii
Saimiri boliviensis
Cebus olivaceus
Cebus capucinus
Brachyteles arachnoides
Ateles geoffroyi
Alouatta seniculus
Alouatta palliata
Pan troglodytes
Gorilla gorilla
Rhinopithecus roxellana
Trachypithecus vetulus
Semnopithecus entellus
Presbytis thomasi
Nasalis larvatus
Procolobus verus
Procolobus badius
Macaca sylvanus
Macaca fascicularis
Macaca fuscata
Macaca mulatta
Macaca sinica
Theropithecus gelada
Papio cynocephalus
Papio anubis
Papio hamadryas
Erythrocebus patas
Chlorocebus aethiops
Cercopithecus campbelli
Cercopithecus mitis
Cercopithecus ascanius
Cynomys ludovicianus
Marmota flaviventris

Figure 2: Phylogenetic tree showing the species included in the analyses. The five transition from habitual female philopatry to habitual female dispersal (X) and the five transitions from habitual female dispersal to habitual female philopatry (O) are also shown.

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296 Table 1: Comparison of species with habitual female philopatry (n = 29) versus species with habitual female

297　　　dispersal (n = 18).

298 All values presented are the median values (and ranges) for the 29 species with habitual female philopatry and the 18 species with

299　　　habitual female dispersal. Significance was assessed by Mann-Whitney tests.

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	habitual female philopatry		habitual female dispersal		
	median	range	median	range	
male tenure length (months)	30	12-120	66	30-144	**W = 71, p-value < 0.001**
age of female first reproduction (months)	41	18-73	40	6-122	W = 224, p-value = 0.42
IR: tenure exceeds AFR (% species)	100		7		**W = 54, p-value < 0.001**
body mass (g)	6450	33-240000	9450	8-400000	W = 227, p-value = 0.46
population density (individuals/kmsquare)	18	0.1-1830	19	0.6-200	W = 259, p-value = 0.97
homerange (ha)	1.2	0.1-58	0.74	0.1-128	W = 245, p-value = 0.73
males per group	3	1-23	2	1-7	W = 318, p-value = 0.21
females per group	8	2-59	5	2-17	W = 344, p-value = 0.07

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