Age-related reproductive success in solitarily and communally nesting female
dormice (*Glis glis*)

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The factors underlying the occurrence of communal nesting in a natural population of fat
dormouse (*Glis glis*) breeding in nest-boxes have been analysed on the assumption that such
behaviour is adaptive. Since co-nesting females were previously shown to be close kin
(prevalently mother–daughter pairs), they were expected to obtain kin-selected benefits not
enjoyed by solitary breeders. The only advantage so far detected accrues to the younger partner,
which gives birth, on average, several days earlier than it would as a solitary breeder and thus
allows its progeny to attain a heavier weight by the time of hibernation. On the other hand, pup
predation in the nest, presumably caused by the older female towards the younger’s litter, was
occasionally recorded. On the whole, it is perhaps more plausible that communal nesting results
from delayed dispersal of yearling females when a high population density limits breeding space,
as proposed for other small rodents.

**Introduction**

Some aspects of the reproductive biology of the fat dormouse (*Glis glis*), a single-brooded
nocturnal and arboreal rodent, are still poorly understood. The species’ long hibernation time
(about seven months) constrains its reproduction between two periods when foraging is critical
for restoring (post-hibernation) or accumulating (pre-hibernation) the animals’ energy reserves
(Storch, 1978; Pilastro, 1990; Pilastro, Gomiero & Marin, 1994). Resources and time, therefore,
are severely limiting, and occasional failure to reproduce in local populations observed in some
years is thought to depend on seasons of scarce production of the principal food items on which
that population depends (Storch, 1978; Pilastro & Marin, unpubl. data).

A study, carried out in a forest in northern Italy on a population of dormice breeding in
artificial nest-boxes (Pilastro et al., 1994), showed that the main factor affecting body mass
of young at weaning and by hibernation (a possible index of short-term reproductive success),
is the date of birth. The majority of births occurred in August, but, even within this relatively
short period, a delay of 7–10 days made a significant difference in young whose mass, by
hibernation, was negatively correlated with the date of birth. On the other hand, the date of
parturition was negatively associated with the female’s weight, possibly because lighter indivi-
duals could not afford lactation until the major food supply (beech seed in our study area) was
at its best (late August–early September). The mother’s body weight influences the timing of
parturition and this, in turn, is the main factor that affects the reproductive success, as shown in
other mammalian species (e.g. Wauters & Dhondt, 1989; Green & Rothstein, 1993).

A puzzling feature in the breeding biology of dormice is the occasional occurrence of
communal nesting (involving two, or rarely three, breeding females), whereas the great majority
of females are solitary breeders (Kahmann, 1965; Santini, 1978; Pilastro, 1992). Communal nests
also occurred in our study population (Marin & Pilastro, 1994; Pilastro et al., 1994). All the female pairs whose relationships were known were found to be close relatives: four adult (two years or more) mothers with their yearling daughters, one adult mother with two yearling daughters, and two yearling sister pairs (Marin & Pilastro, 1994). Therefore, kin-selected advantages are expected to accrue to communally breeding females (Hamilton, 1964). A preliminary search for costs and benefits brought about by this behaviour did not show any significant difference in the average body mass of the mother, litter size per female, or body mass of pups, between communal and single nests (Pilastro et al., 1994).

In this species, body mass of yearling females is on average lower than that of older females (Kahmann, 1965; Storch, 1978; Pilastro, 1992), and communal nests are often formed by one yearling and one adult female (Marin & Pilastro, 1994). We analyse some reproductive success parameters (i.e. litter size, date of birth, litter body mass at weaning, and mortality rate at nest) of females at their first breeding season and of older females, and we evaluate whether communal nesting decreases or removes such differences.

Materials and methods

The study was conducted in the Cansiglio Regional Forest, on the southern part of the Alps, northern Italy. We used 2 sites (30 and 12.5 ha, respectively) located at an altitude of 1000 m, part of a large woodland (670 ha) dominated by beech (Fagus sylvatica), which is locally mixed with spruce (Picea abies), fir (Abies alba), and sycamore (Acer pseudoplatanus). In spring 1990, 100 artificial nest-boxes were set in the first site and 50 in the second one. The nest-boxes were checked every 2–3 weeks between June and November during daytime. During the breeding season (from late July to mid-September) nest-boxes were checked more frequently. In 1991, female dormice used boxes for nesting only in the first site, whereas in 1992 they were found breeding in both sites. All the data presented here refer to the first site. The studied population is intermediate between the nominal subspecies G. g. glis and the peninsular subspecies G. g. italicus (Witte, 1962).

All the individuals found in the nest-boxes were aged, when possible, in 3 classes (born during the year, first year, and older, later on referred to as young, yearling, and adult, respectively), and sexed according to König (1960) and Vietinghoff-Riesch (1960). Yearling individuals could be told apart from older ones only when they were found in the first part of the active season, when the moult from first-year to adult fur is not yet completed (Homolka, 1978; Franco, 1989). Body mass was measured with a Pesola spring balance to the nearest gram; age of pups at nest (expressed in days) was estimated according to König (1960) and Vietinghoff-Riesch (1960). Only litters found within the first week after parturition were aged. At this time, we also weighed the mother, and the body mass after parturition has been taken as an indicator of the condition of the mother. Litters in communal nests could be told apart by a difference in age. Adults were marked by toe-clipping. Ethylchlordane was used locally as an anaesthetic and haemostatic powder to prevent bleeding, when necessary. Only occasionally did animals react as if hurt. Pups in the nest and most of the young were individually marked using ear tags with consecutive numbers (Ohrmarken Hauptner) (Pilastro, 1992). Both adults and young, after weighing and marking, were put back in the box. We marked 265 individuals in 1991 (53 adult males, 47 adult females, and 165 young) and 629 individuals in 1992 (90 adult males, 123 adult females, and 416 young). To measure the body mass of pups before weaning, litters were reweighed, when about 25 days old. This age was selected because it was about 10 days before complete weaning (König, 1960), in order to minimize the risk of nest desertion, observed in previous studies (König, 1960; Santini, 1978; Pilastro, 1992). Since mass increase is roughly linear in this period (Vietenhoff-Riesch, 1960; Pilastro, 1992), we corrected the mass of pups in all litters up to 3 days older or younger than 25 to this date. The mother was weighed again at this stage to measure the variation of the body mass during lactation,
Table I

Variation of some reproductive parameters in relation to the age of the mother. Means (S.D., n) are given

<table>
<thead>
<tr>
<th>Year</th>
<th>Yearling</th>
<th>Adult</th>
<th>Statistic</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>1991 Mother body mass</td>
<td>127.5 (8.54, 12)</td>
<td>155.3 (14.41, 24)</td>
<td>F = 37.8</td>
<td>0.00001</td>
</tr>
<tr>
<td></td>
<td>Litter size</td>
<td>4.68 (1.34, 19)</td>
<td>5.79 (1.17, 28)</td>
<td>F = 9.0</td>
</tr>
<tr>
<td></td>
<td>Date of parturition</td>
<td>10/8 (4.97, 19)</td>
<td>6/8 (4.39, 28)</td>
<td>F = 11.7</td>
</tr>
<tr>
<td></td>
<td>Mean litter body mass</td>
<td>29.4 (5.08, 14)</td>
<td>28.5 (4.39, 15)</td>
<td>F = 0.25</td>
</tr>
<tr>
<td></td>
<td>Mother body mass variation</td>
<td>+7.6 (9.06, 6)</td>
<td>-5.5 (5.64, 11)</td>
<td>H = 6.8</td>
</tr>
<tr>
<td>1992 Mother body mass</td>
<td>125.5 (15.27, 24)</td>
<td>144.3 (17.00, 24)</td>
<td>F = 16.37</td>
<td>0.0002</td>
</tr>
<tr>
<td></td>
<td>Litter size</td>
<td>5.03 (1.18, 29)</td>
<td>6.22 (1.89, 27)</td>
<td>F = 8.09</td>
</tr>
<tr>
<td></td>
<td>Date of parturition</td>
<td>23/8 (6.62, 29)</td>
<td>15/8 (7.98, 27)</td>
<td>F = 13.53</td>
</tr>
<tr>
<td></td>
<td>Mean litter body mass</td>
<td>31.6 (5.15, 14)</td>
<td>31.2 (5.58, 20)</td>
<td>F = 0.06</td>
</tr>
<tr>
<td></td>
<td>Mother body mass variation</td>
<td>+9.56 (5.52, 11)</td>
<td>+5.07 (7.37, 18)</td>
<td>H = 2.48</td>
</tr>
</tbody>
</table>

1 Analysis of variance (ANOVA); for mother body mass variation during lactation a non-parametric test was used (Kruskal- Wallis test)
2 Within one week after parturition
3 Statistics were computed using the number of days after January 1st and then converting it to the corresponding date
4 At the 25th day
5 Body mass variation between the first week after parturition and the 25th day, expressed as percentage of the first body mass value

which was computed as follows:

\[ \frac{[(M_w - M_p)/M_p] \times 100}{\text{where } M_p \text{ is the body mass of the mother within a week of parturition and } M_w \text{ is the body mass of the mother when pups were 25 (± 3) days old. Body mass variation between parturition and weaning has been taken as an index of the cost of lactation (Price & Boutin, 1993).}} \]

Mortality rate was computed as the difference in the number of pups at nest between the first and the last check. Since nests were kept under observation for different periods of time, the probability of observing a mortality event, involving one or more pups, was not the same for all nests. We therefore corrected the mortality rate according to Mayfield's method (1975). Briefly, this method treats nests in terms of survival probability over a period of time. The probability of observing a loss of one young is a function of the number of pups in a given nest and of the length of the period of observation. For this computation, only nests whose observation period fell within the first 30 days after birth were considered, and therefore the mortality rate is the average rate from birth to this time.

Mortality of one or more pups at nest might in theory affect, either positively or negatively, surviving probability of the rest of the litter. Mortality and survival data are not therefore fully independent observations. For this reason, degrees of freedom might be inflated and statistical probabilities of the tests on difference of mortality rates might be overestimated. Since neither the cause of the observed mortality at nest nor its effect on surviving pups is known (and consequently the real degrees of freedom), there is no realistic alternative for treating mortality data, but the statistical significance of the test must be considered cautiously. Mortality rate was also indicated as the proportion of litter affected by mortality,
Table II

Variation of some reproductive parameters in relation to the age of the mother and to the social structure of the nest in 1992. Means (S.D., n) are given; different indices refer to significant difference between means (Least Significant Difference multiple range test, P < 0.05)

<table>
<thead>
<tr>
<th></th>
<th>Solitary nests</th>
<th>Communal nests</th>
<th>Statistic</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Yearling</td>
<td>Adult</td>
<td>Yearling</td>
<td>Adult</td>
</tr>
<tr>
<td>Mother body mass²</td>
<td>124.5³</td>
<td>145.4³</td>
<td>123.3⁴</td>
<td>146.3⁴</td>
</tr>
<tr>
<td></td>
<td>(12.25, 17)</td>
<td>(17.69, 18)</td>
<td>(16.66, 7)</td>
<td>(16.29, 6)</td>
</tr>
<tr>
<td>Litter size²</td>
<td>4.85⁵</td>
<td>6.75⁶</td>
<td>4.89⁶</td>
<td>5.43⁶</td>
</tr>
<tr>
<td></td>
<td>(1.09, 20)</td>
<td>(1.77, 20)</td>
<td>(1.17, 9)</td>
<td>(1.62, 7)</td>
</tr>
<tr>
<td>Date of parturition¹</td>
<td>26/8⁷</td>
<td>16/8⁸</td>
<td>18/8⁹</td>
<td>13/8⁹</td>
</tr>
<tr>
<td></td>
<td>(6.63, 20)</td>
<td>(8.87, 20)</td>
<td>(3.16, 9)</td>
<td>(4.57, 7)</td>
</tr>
<tr>
<td>Mean litter body</td>
<td>32.0</td>
<td>31.2</td>
<td>31.1</td>
<td>31.2</td>
</tr>
<tr>
<td>mass⁴</td>
<td>(5.17, 8)</td>
<td>(5.90, 14)</td>
<td>(5.58, 6)</td>
<td>(5.29, 6)</td>
</tr>
<tr>
<td>Mother body mass</td>
<td>± 9.49</td>
<td>± 5.08</td>
<td>± 9.70</td>
<td>5.02</td>
</tr>
<tr>
<td>variation³</td>
<td>(5.26, 7)</td>
<td>(6.74, 13)</td>
<td>(6.80, 4)</td>
<td>(9.72, 5)</td>
</tr>
</tbody>
</table>

¹ One-way analysis of variance (ANOVA); for mother body mass variation during lactation a non-parametric test was used (Kruskal-Wallis test)
² Within one week after parturition
³ Statistics were computed using the number of days after January 1st and then converting it to the corresponding date
⁴ At the 25th day
⁵ Between the first week after parturition and the 25th day, expressed as percentage of the first body mass value

which are independent data. This treatment of mortality data, on the contrary, implies a substantial loss of information and a drastic reduction of the degrees of freedom, increasing the risk of accepting the null hypothesis when it is not true.

Since mother body mass, date of parturition, mean litter body mass at weaning, and mortality rate differed significantly between the 2 years (Pilastro et al., 1994), data from the 2 seasons were analysed separately. Significant differences of mortality rate between years, age classes, and communal and solitary nests were tested by comparing the observed frequencies with those expected on the basis of the number of pups observed, times the days of observation (Mayfield, 1975), using a G-test for goodness of fit (Sokal & Rohlf, 1981).

Results

In 1991, 51 females bred in the nest-boxes and two shared the same nest. In 1992, 28 shared nests, out of 77 that bred in boxes. Summing over the two years: of a total of 112 nests, 98 were solitary, and 14 were communal, 12 with two and two with three breeding females. Among the 47 breeding females that could be aged in 1991, 19 (40.4%) were yearlings. In 1992, of 56 females that could be aged, 29 (51.8%) were yearlings. A similar proportion of yearling females was found in communal nests (9 out of 16, 56.3%).

On average, adult breeding females were 15–20 g heavier, gave birth one week earlier, and produced more numerous litters than did yearling females (Table I). No significant difference was found between adult and yearling females in the mean body mass of pups at weaning. The cost of lactation, measured as the variation of mother body mass between parturition and weaning, was higher in the adults, but this difference was significant only in 1991. When age-related reproductive success was analysed separately for communal and solitary nests (Table II), this figure remained essentially the same. The only difference was in the date of parturition, significantly earlier for yearling females in communal nests than it was for solitary breeders of the same age.
Table III
Average estimated mortality of pups at nest during their first 30 days of life in relation to the age of the mother

<table>
<thead>
<tr>
<th></th>
<th>1991</th>
<th>1992</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age of the mother</td>
<td>yearling</td>
<td>adult</td>
</tr>
<tr>
<td>Pups born</td>
<td>59</td>
<td>90</td>
</tr>
<tr>
<td>Pups disappeared</td>
<td>11</td>
<td>3</td>
</tr>
<tr>
<td>Nests</td>
<td>12</td>
<td>16</td>
</tr>
<tr>
<td>Days of observation × pups</td>
<td>914</td>
<td>1593</td>
</tr>
<tr>
<td>Mortality rate¹</td>
<td>30.5%</td>
<td>5.5%</td>
</tr>
</tbody>
</table>

¹Corrected for the number of pups observed and the number of days of observation (see Materials and methods)

In 1991, overall pup mortality at the nest was lower than in 1992 (Table III, G = 10.78, d.f. = 1, P < 0.001, G-test for goodness of fit). In both years, litters of yearling females suffered higher mortality at the nest than did those of adult females (G = 10.37, d.f. = 1, P < 0.01 for 1991; G = 7.25, d.f. = 3, P < 0.01 for 1992). In 1992, when litters of adult and yearling females were analysed separately in solitary and communal nests (Table IV), the difference of pup mortality between yearling and adult mothers was significant only in communal nests (G = 8.60, d.f. = 1, P < 0.01), but not in solitary nests (G = 0.932, d.f. = 1, n.s.). The difference of mortality rate observed in communal nests was due to the disappearance of two whole litters belonging to the yearling female. Mortality rate of pups in communal nests, as a whole, was not significantly different from that observed in solitary nests (G = 0.71, d.f. = 1, n.s.). Mortality rate observed in litters of yearling females in communal nests was greater than that observed in litters of their counterparts in solitary nests, but the difference was not significant (G = 1.15, d.f. = 1, n.s.). The differences of mortality rate between litters of adult females in communal and in solitary nests were not significant (G = 1.77, d.f. = 1, n.s.). No difference in mortality rate resulted significantly when it was expressed as proportion of litters affected by mortality (Tables III and IV).

Discussion
In our population, the reproductive success of females at their first breeding season was significantly lower than that of adult females, both in terms of litter size and date of parturition.

Table IV
Average estimated mortality of pups at nest during their first 30 days of life in 1992 in relation to the age of the mother and to the social structure of the nest

<table>
<thead>
<tr>
<th></th>
<th>Solitary nests</th>
<th>Communal nests</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pups born</td>
<td>36</td>
<td>93</td>
</tr>
<tr>
<td>Pups disappeared</td>
<td>8</td>
<td>15</td>
</tr>
<tr>
<td>Nests</td>
<td>7</td>
<td>14</td>
</tr>
<tr>
<td>Days of observation × pups</td>
<td>528</td>
<td>1527</td>
</tr>
<tr>
<td>Mortality rate¹</td>
<td>36.7%</td>
<td>25.6%</td>
</tr>
</tbody>
</table>

¹Corrected for the number of pups observed and the number of days of observation (see Materials and methods)
Mean body mass of litters at weaning did not differ significantly between these two age classes, despite the larger litters delivered by adult females. Similar results were found when reproductive success was analysed on the basis of the body mass of the mother (Pilastro et al., 1994). First year females, after parturition, were on average about 30 g lighter than adult females, and their weight was always more than 110 g. Non-breeding first year females were found whose body mass was lower, in some cases less than 85 g (Pilastro, unpubl. data). It seems that a weight threshold exists for females to reproduce, and that the female body mass is a major factor influencing reproductive success in this species. Body mass of young before hibernation strongly depends on their date of birth, early born pups weighing much more than late born ones. The date of parturition depends, in turn, on the body mass of the mother (Pilastro et al., 1994); since body mass of young after hibernation is positively correlated with their body mass by hibernation, and negatively correlated with their birth date (Pilastro, unpubl. results), an early birth is likely to confer an advantage to young and to have a persistent influence on their reproductive success, as observed in other mammals (Green & Rothstein, 1993).

Solitary nesting is the common breeding pattern of female dormice, but communal nests are found regularly. Frequency of communal nesting, in our experience, was variable between years, ranging from less than 5% of the total number of breeding females, up to 50% (Pilastro, 1992; Pilastro et al., 1994). This variation did not seem to depend on shortage of nest-boxes, since unoccupied boxes were always present and nest-shifting from boxes to natural dens, and vice versa, occurred frequently (Pilastro et al., 1994).

The fact that in our study co-operatively breeding females were close kin (Marin & Pilastro, 1994) can be interpreted in two ways. It may be the result of kin selection acting by increasing the benefits/costs ratio for co-nesting females through an increment of their inclusive fitness. Or, it may result from philopatric behaviour of those young females whose dispersion was delayed. In the first case, we would expect females actively to seek close relatives as partners for nesting, and the frequency of co-operative breeding to be limited mainly by the availability of close relatives (mothers, daughters, or sisters). In the second case, co-nesting could be the consequence of delayed dispersal of young females in poor physical conditions, unable to face the costs of dispersal, or an alternative reproductive tactic in response to limited space due to high population density.

If communal nesting was mainly driven by kin selection, a substantial benefit, compared to single nesting, would be expected to accrue to at least one of the partners, even if it carried a cost for the other. As a whole, average reproductive success of communally breeding females should be higher than that of solitary females. In some laboratory studies on small rodents it was found that the presence of two mothers and their litters in the same nest improved the growing rate of pups, as compared to that of pups in litters raised singly (Sayler & Salmon, 1969; Solomon, 1991; König, 1994). On the other hand, a detailed field study on two species of Peromyscus (Wolff, 1994) failed to show any benefit of communal nesting. Results presented in this and in previous studies (Pilastro et al., 1994; Marin & Pilastro, 1994) have failed, so far, to show a clear advantage for nesting communally. In fact, average reproductive success (in terms of litter size, mean litter body mass, and timing of reproduction) did not change significantly between females nesting communally and those nesting solitarily. However, when the age of breeding females was considered, we found that communally breeding first year females bred earlier than their counterparts (Table II). In a breeding season 'compressed' as that of dormice, this time difference produces a substantial increase in the weight of young at the time of hibernation (Pilastro et al., 1994), and fat reserves in hibernating females are likely to determine their survival probability (as observed in other hibernating species, e.g. Sauer & Slade, 1987), and their
breeding success in the following year. On the other hand, in a few cases the younger partner of a communally nesting pair seemed to suffer a higher, although not significant, predation cost on her litter than if she bred singly. Direct evidence on the causes of such mortality are lacking, but the disappearance of some pups from one mother’s litter without any loss from the litter of the other seems to exclude predation from outside the nest (e.g. pine marten Martes martes, weasel Mustela nivalis or conspecific males). Pup mortality might depend on inter-litter competition, as observed in the rat when litters of different age are reared in communal nests (Mennella et al., 1990). This would explain the higher mortality rate of the young partner’s pups, which are on average one week younger than those born by the older female (Table III). Alternatively, mortality may be due to the mother, or, more likely, to the partner female. Pup cannibalism is a common behaviour in rodents (Gandelman & Simon, 1977; Fuchs, 1982; Elwood, 1992; König, 1994), and a similar behaviour of reproducing females, killing each other’s young, has been described also for prairie dogs (Hoogland, 1985) and for communally nesting birds (Vehrencamp, 1977; Mumme, Koenig & Pitelka, 1983). It is still uncertain whether, in communal nesting dormice, the older partner reduces the litter of her daughter. Such infantilicidal behaviour would result in a re-distribution of milk from alien to own young, since females in communal nests seem to suckle young from both litters (Pilastro, 1992). In our study, predation on their litters did not cause the yearling females to flee, and they have been found later in the nest, presumably as helpers, even when their litter had disappeared entirely.

The alternative explanation to communal nesting, i.e. that it results from delayed dispersion, is perhaps more likely. If delayed dispersion involved mainly physically inferior individuals, first year females in communal nests should have, on average, lower body mass than their counterparts, considering that mother body mass is among the most important determinants of breeding success in the female dormouse (Pilastro et al., 1994). In our study, communal nesting always included at least one yearling female, but our data showed no significant difference between the mean weight of yearling females breeding in communal nests and that of yearlings breeding in solitary nests. This seems to exclude that delayed dispersal is a consequence of the bad body conditions of the young female. In some microtine rodents, it has been proposed that communal nesting results from delayed dispersal of young and local grouping of related females, in response to a limitation in breeding space (Lambin & Krebs, 1991; Wolff, 1992). In this case, a correlation would be observed between frequency of communal nests and population density, and no effect on the reproductive success (or a negative one). In our study, over a total of five reproductive seasons, the highest frequencies of communal nests were observed in years with the highest population densities (Pilastro, 1992; Pilastro et al., 1994), supporting the idea that delayed dispersal and nesting with their mothers may be an alternative reproductive tactic of yearling females in response to limited space. In this case, kinship would certainly favour such a ‘choice’.

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REFERENCES


