# INFANTICIDE IN THE EVOLUTION OF REPRODUCTIVE SYNCHRONY: EFFECTS ON REPRODUCTIVE SUCCESS

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**Synchronous breeding in animals and plants has stimulated both a theoretical and empirical examination of the possible benefits of active synchronization. The selective pressures of predation and infanticide are the strongest candidates proposed to explain the evolution of reproductive synchrony. Alternatively, breeding asynchronously with conspecifics may ensure a greater availability of resources per breeder. However, the possible fitness benefits resulting from active asynchronization have not yet received attention in evolutionary ecology. Here we present a hypothesis, based on a graphical model, illustrating the costs and benefits of the two modes of reproduction. We tested the hypothesis empirically using a 2 × 2 full factorial study design, where reproductive synchrony and infanticide tactics were manipulated in enclosed populations of the bank vole. The results reveal a relationship between infanticide tactics and breeding synchrony as illustrated by our hypothesis. In general, female reproductive success (number and size of offspring surviving to weaning) was significantly lower in infanticidal populations. Moreover, an asynchronous breeding pattern proved to be advantageous in the noninfanticidal population but this advantage of asynchrony was lost as infanticide became common in the population. Our findings support the idea that synchronous reproduction could have evolved as a counterstrategy against infanticide.**

**KEY WORDS: Breeding synchrony, infanticide tactics, mammals, *Myodes glareolus*, reproductive strategies.**

By adjusting the time of reproduction to occur asynchronously with conspecifics that utilize the same resources, breeding females appear to exploit an advantageous strategy that reduces breeding density and staggers the population's resource requirements (McShea 1989). However, except for limited evidence provided by Lambin (1993), direct support for a positive effect of asynchronous breeding on reproductive success is lacking. Instead, for decades broad attention has focused on the tendency of female groups in many taxa to show a pronounced synchrony

in reproductive events (e.g., ovulation, menstruation or parturition), that is expressed at higher levels than expected due to environmental seasonality (in humans see e.g., McClintock 1971; Graham 1991; Weller et al. 1999; other animals e.g., Hailman 1964; Kummer 1968; McClintock 1978; Dunbar 1980; Findlay and Cooke 1982; Wallis 1985; Lambin 1993; Heliövaara et al. 1994; Behncke 2000; Spencer et al. 2001). In communal breeders, the advantages of synchronous breeding might be connected with more efficient foraging (Emlen and Demong 1975), female

cooperative nursing (Rood 1978, 1980; Brown 1987; Boyce and Boyce 1988; Mennella et al. 1990), or paternal care (Knowlton 1979). In noncommunal breeders, reproductive synchrony is often explained by the predation model (Darling 1938), which predicts that simultaneous offspring production decreases the probability of predation on any particular young due to a more efficient collective defense and the limited ability of predators to hunt (confusing effect) and consume (swamping effect) the overabundant prey (Rutberg 1987). The swamping hypothesis in particular has been put forward to explain mast fruiting in plants (Janzen 1971; Silvertown 1980) and reproductive synchrony in birds (Findlay and Cooke 1982) and mammals (Rutberg 1987). However, the conditions required for the predation model to support a synchronous breeding pattern may not be realized. For instance, in contrast with conventional wisdom, highly asynchronous reproduction may be the best strategy when predators have a typical generalist-type functional response (Ims 1990b), due to the ability of generalist predators to prey upon a variety of prey. As the density of main prey decreases, the functional response of generalist predators is to switch to the alternative prey (Holling 1959). Therefore, considering offspring predation and breeding synchrony, the predation pressure from generalist predators on offspring may actually decrease as the degree of asynchrony increases. For specialist predators, the functional response is the opposite, but only few predators are probably able to specialize solely on offspring predation (Ims 1990b).

More recently, the avoidance of offspring loss due to infanticide has been proposed as a potential explanation for the evolution of reproductive synchrony (Lambin 1993). Infanticidal behavior is an intrinsic feature present extensively in mammalian populations (in humans see e.g., Pitt and Bale 1995, in other animals Hrdy 1979; Hausfater and Hrdy 1984; Parmigiani and vom Saal 1994; Ebensperger 1998; van Schaik and Janson 2000). In many mammalian populations, infanticide is considered to be the main or a significant cause of juvenile mortality (Boonstra 1978; Sherman 1981; Packer and Pusey 1983; Caley and Boutin 1985; Hoogland 1985; Borries 1997; Lambin and Yoccoz 1998), and there are some indications from previous studies that infanticidal behavior might be heritable (Svare et al. 1984; Perrigo et al. 1993). Infanticidal behavior is blocked in infanticidal small rodent females around the time of parturition (house mice: *Mus musculus*: McCarthy and vom Saal 1985; Soroker and Terkel 1988; Wolff and Macdonald 2004; bank vole: T. Poikonen, E. Koskela, and T. Mappes, unpubl. ms.), enabling synchronous breeding to possibly act as a counterstrategy against infanticide committed by other females. Experimental studies in rodents have also shown that male infanticidal behavior is blocked for the period from parturition to the infant stage of the litter that he has sired (vom Saal and Howard 1982; Brooks and Schwarzkopf 1983; vom Saal 1985; McCarthy and vom Saal 1986; Mennella and Moltz 1988;

Soroker and Terkel 1988; Cicirello and Wolff 1990). Therefore, synchronous breeding could minimize the risk of both female and male infanticide. Studies on the determinants of reproductive synchrony in the Townsend's vole (*Microtus townsendii*) (Lambin 1993), and on territorial behavior and reproductive success in the bank vole (Koskela et al. 1997) suggest that the potential of synchronous breeding to act as a counterstrategy against infanticide exists, but direct studies on the interaction between synchrony and infanticide have not yet been carried out.

The reproductive benefits of greater resource availability per breeder versus the risk of infanticide are illustrated for a model species, an infanticidal small rodent, the bank vole (*Myodes glareolus* Schreber), in Figure 1. The curves represent the energy requirements of reproducing females, because food (energy) is crucial for successful reproduction in small rodents (e.g., Duquette and Millar 1995; Koskela et al. 1998). We represent energy rather than space, as habitats are not usually homogeneous and consequently, the total area required to provide enough resources for successful reproduction may not be directly proportional to the number of individuals breeding, whereas the energy required by a population increases with an increasing number of reproducing females. We also recognize that in addition to greater availability of resources, an increase in space may also provide other benefits for reproductive success (e.g., less aggression between adjacent females). In the model, females are assumed to reproduce in postpartum estrus, which is usually the case in microtine rodents in the wild (Hasler 1975; Bronson 1989). We hypothesize that within noninfanticidal populations (NON-INF) (Fig. 1A, B), an asynchronous breeding mode (AS) (Fig. 1A) should be beneficial in terms of reproductive success compared to a synchronous (S) one (Fig. 1B), due to the lower total energy requirement of the female population during peak lactation. Within the infanticidal population (INF) (Fig. 1C, D), the synchronously breeding population (S) (Fig. 1D) has infanticide-free periods following each synchronized parturition and is hypothesized to face similar costs and benefits to the noninfanticidal synchronous population (Fig. 1B). The situation is predicted to be reversed in the asynchronously breeding infanticidal population (INF/AS) (Fig. 1C), because the female population has a lower energy requirement, but infanticidal females are constantly present in the population.

To test this hypothesis, we determined the reproductive gains for female bank voles adopting different infanticide and breeding strategies. We manipulated both reproductive synchrony (by mating females at different times) and infanticide tactics by selecting only infanticidal or noninfanticidal individuals to form the study populations. In wild bank vole populations, about two-thirds of nonreproducing females exhibit infanticidal behavior (T. Mappes, unpubl. data) and therefore sufficient individuals were available to create experimental populations of solely infanticidal or noninfanticidal individuals. Although there is no firm evidence on
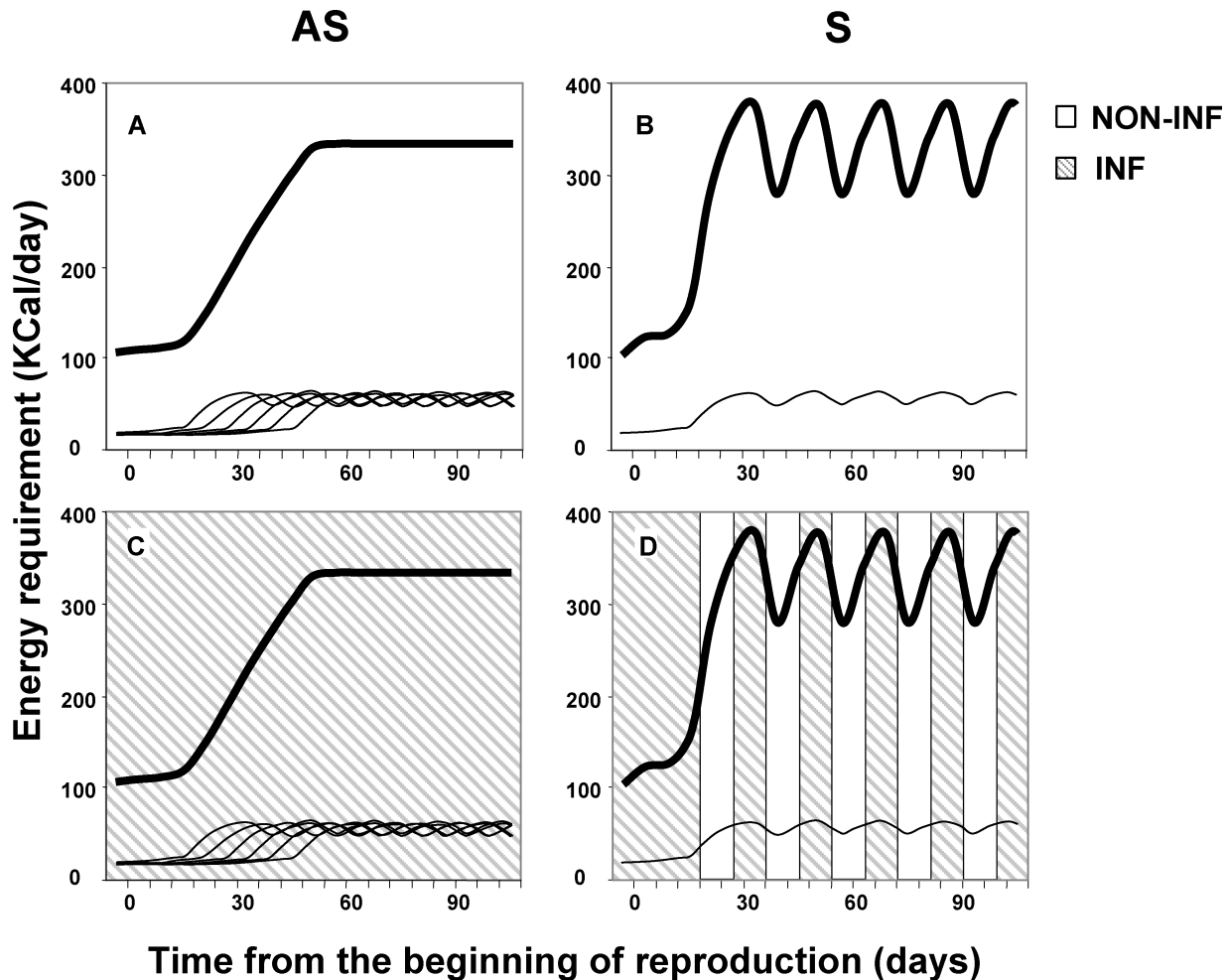
**Figure 1.** Graphical illustration of resource availability per breeder/risk of infanticide balance associated with different reproductive tactics. (A, C) asynchronously and (B, D) synchronously breeding populations of six bank vole females. Thin lines (—): energy requirement of individual reproducing females; thick lines (—): total energy requirement of the female population; shaded areas = females in the population are in an infanticidal stage; blank areas = females are noninfanticidal or infanticide is blocked (see Study Species). In noninfanticidal populations (A, B), asynchronous reproduction leads to a greater access to resources (energy) per breeder (A) as compared to the synchronous mode (B). In infanticidal populations (C, D), the asynchronously enhanced access to resources is traded off against the risk of offspring loss due to infanticide. Estimates of energy requirements are based on Kaczmarski 1966.

the degree of breeding synchrony in wild bank vole populations, this commonly used small rodent species provides an excellent potential to manipulate breeding synchrony/asynchrony, and thus is a suitable species to experimentally test the assumptions of the graphical model. The model is based on the conventional assumption in history theory that resources are limited for organisms, as usually is the case in the nature. As long as resources are not limited, individuals and populations are expected to increase their intake. Although the shortage of energy resources during midsummer for foliage-eating microtines appears unlikely, omnivorous microtines (e.g., the bank vole), a lack of food may limit reproductive success (Koskela et al. 1998). The energy demands of breeding females are 30%–130% higher than those of nonreproducing females of the same body size (Migula 1969; Grodzinski

and Wunder 1975) and thus, simultaneous breeding can increase the energy need of a population dramatically, particularly so if population density is high.

The following predictions were addressed: First, if asynchronous breeding provides an energy benefit, we should expect higher reproductive success for asynchronously breeding females over synchronously breeding females in the noninfanticidal population (NON-INF/AS vs. NON-INF/S). Second, if infanticide is costly, individual fitness should be lower in the infanticidal population compared to the noninfanticidal population (INF vs. NON-INF). Third, if synchronous breeding acts as a counterstrategy against infanticide, breeding success should be lower in the infanticidal population compared to the noninfanticidal population among asynchronously reproducing individuals (INF/AS vs.

NON-INF/AS), whereas synchronous breeding should counteract the detrimental effects of infanticide on fitness (INF/S vs. NON-INF/S).

## Methods

### STUDY SPECIES

Our study species, the bank vole is a microtine rodent showing significant heritability (0.564 ± 0.018 SE) of female infanticidal behavior (see below). The frequency of infanticide tactics may differ according to population density or spatial and temporal variation in food competition, but to the best of our knowledge, the effects of these factors have not been tested in the bank vole or in other rodents. Female infanticidal behavior is blocked on average 0–1 days before parturition and it resumes again on average 7–10 days after parturition (T. Poikonen, E. Koskela and T. Mappes, unpubl. ms.). Bank voles have a polygynandrous breeding system (Mills et al. 2007). Females breed in postpartum estrus, that is can become pregnant within a few hours after parturition. Thus, for individual females, reproductive events such as parturition can occur at regular intervals throughout the breeding season. Females give birth to up to four litters during the breeding season, the litter size ranging from 2–10 (on average 5) (Koivula et al. 2003). Pregnancy lasts for 18–20 days and lactation on average for 18 days.

For successful breeding, space and food resources are crucial for females (e.g., Koskela et al. 1998; Jonsson et al. 2002). Breeding bank vole females defend an exclusive territory (breeding area) against other females and they do not exhibit communal nursing, but their home ranges (feeding areas) greatly overlap (Koskela et al. 1997). In comparison, males have territories overlapping with several female territories (Mazurkiewicz 1971). Although female territoriality could act as a counterstrategy against infanticide, the defense against intruders is never fully complete and this behavior alone is inadequate to totally prevent infanticide in the bank vole. This is the case in many other mammals as well, where infanticide by intruders occurs despite of territorial behavior and, additionally, sometimes despite of cooperative nursing and defense by kin/family in the group/herd (see e.g., Sherman 1981; Packer and Pusey 1983; Hoogland 1985). Female bank voles are solitary breeders and do not receive cooperation during nursing from neither male nor kin, and thus the litter must occasionally be left without immediate guarding (e.g., during foraging by the mother). As characteristic for mammals, bank voles are able to identify sex, age, and reproductive state of neighboring individuals by using odor signals (reviewed in Osipova and Rutovskaya 2000). These signals may act as cues to synchronize / asynchronize breeding with the other females in the population. Both breeding synchrony and active asynchrony may occur in small mammals (Ims 1987; McShea 1989), however, to the best of our knowledge, the distribution of breeding events has not been studied in natural bank vole populations.

### LABORATORY AND FIELD PROCEDURES

#### Individual infanticidal status

The infanticidal behavior of all bank vole individuals (second-generation laboratory stock from wild ancestors) was tested in the Experimental Animal Unit of the University of Jyväskylä using the neutral arena procedure (Labov et al. 1985). All tested individuals were in a nonreproducing stage (neither gravid nor lactating). A newborn pup was placed in the middle of a 43 × 26 × 15 cm standard mouse cage with a thin layer of clean sawdust, and an adult test individual was introduced into the cage and placed under continuous observation. If the adult aggressively attacked the pup during the 30-min observation period it was considered infanticidal. Usually the infanticidal individuals indicated clear aggression against the pup within 10 min, whereas noninfanticidal individuals typically inspected the pup several times during the test but caused the pup no harm. If aggression against the test pup was expressed, the pup was immediately removed from the test arena and euthanized. High repeatability of infanticidial behavior of the testing procedure (89%) was confirmed by testing 44 individuals twice ($\chi^2 = 26.3$, $P < 0.001$). The experiments were conducted with the permission of the Ethical Committee of Scientific Animal Experiments and the Provincial Administrative Board of Western Finland.

Genetic parameters (e.g., heritability estimates) of infanticidal behavior were analyzed in the separate study (T. Mappes, J. Aspi, E. Koskela, S. Mills, T. Poikonen and J. Tuomi, unpubl. ms.). In the analyses, we used the infanticidal status for 418 females and their mothers. The heritability estimates are narrow-sense $h^2$ estimates examined in the laboratory using an outbred wild stock of bank voles. All tested females were in a nonreproducing stage. The laboratory tests were performed in neutral arena (see above). We assumed that infanticide is a polygenically and environmentally determined character and applied the "threshold" model (e.g., Falconer and Mackay 1996; Roff 1997; Lynch and Walsh 1998) to estimate the genetic parameters for it. The threshold model posits that the determination of the discontinuous variation in a character is a consequence of some underlying character, called the liability, that is itself continuously distributed. The model proposes that at some point along the liability distribution of a continuous trait, a threshold exists past which an individual shows the phenotypic character. Here, genetic parameters of liability could be estimated using data on the incidence of infanticidal behavior among mothers and the incidence among daughters. We estimated the parent–offspring regression for the liability of infanticide using the equation derived from Reich et al. (1972):

$$t = \frac{X - X_R\sqrt{\left[1 - \left(X^2 - X_R^2\right)\left(1 - (X/i)\right)\right]}}{i + X_R^2\,(i - x)},$$

where $i$ is the mean deviation of infanticidal individuals from the population mean, and $X$ and $X_R$ are the normal deviates of population and offspring of the threshold from the mean. Consequently, the heritability for females ($h^2$) was estimated as $2t$.

### Experimental design

The experiment was carried out at Konnevesi, central Finland (62°37N, 26°20E) in 20 outdoor enclosures (0.2 ha each) (for details on the vegetation and construction of enclosures (see Oksanen et al. 2003). To test the predictions of our hypothesis (Fig. 1), four respective treatment groups were formed. A large set of females were mated in the laboratory by pairing them with a random male in standard breeding cages for two days. The pairings were carried out in two sets with a nine-day interval to create the two groups, the synchronously and asynchronously breeding groups. Females that copulated successfully (determined by the presence of a copulatory plug) were used in the experiment. Females were released into outdoor enclosures on approximately day 2 of their pregnancy so that in the synchronously breeding enclosures (S), all females would give birth simultaneously. The asynchronous enclosures (AS), were formed by releasing half of the females on day 11 of their pregnancy and the other half on day 2 of their pregnancy so that the former would give birth as the latter were still approximately in the middle of their pregnancy (day 9 of their 18–20 day pregnancy). Twelve of the enclosures consisted of only noninfanticidal females, and eight enclosures consisted of only infanticidal females, forming the noninfanticidal (NON-INF) and infanticidal (INF) populations, respectively. The initial densities in the enclosures were equal (six adult females and four noninfanticidal males per enclosure, males were released one day after females; males used in all experimental groups were noninfanticidal to focus solely on the risk of female infanticide), that is 30 females/ha, or 50 individuals/ha (both sexes), which is higher than natural bank vole density in a nonpeak phase of their population cycle (Koivula et al. 2003). Because some females failed to raise any young to independence, the density of reproducing females differed between enclosures, being on average 3.2 breeding females/enclosure, that is 16 breeding females/ha.

Two to three days prior to the expected date of parturition, females were captured and brought to the laboratory in order that litter sizes and body measurements (weight, head width) of the pups could be recorded at birth. Trappings were performed in each enclosure with 20 multiple-capture live traps that were distributed in $5 \times 4$ grid (10 m apart from each other). The newborn pups were individually marked by toe-codes to identify them at weaning age. Females with newborn litters were returned to the enclosures at the site of capture (Mappes et al. 1995a). Based on

the day of copulation in the laboratory as well as the visual cues of pregnancy in the field we could accurately estimate the day of delivery. When the offspring were approximately 30-day old, populations were trapped to record the individual survival of the offspring to independence, and their weaning weight and head width were measured. According to our earlier studies on bank voles, a larger size at weaning indicates higher offspring quality, in terms of for example earlier maturation rate and higher survival (Mappes et al. 1995b). At the beginning of the experiment, there were no differences in the original litter sizes, ages, or relatedness between the females in different treatment groups (litter size: infanticide: $F_{1,116} = 0.187$, $P = 0.667$; synchrony: $F_{1,116} = 0.014$, $P = 0.905$, infanticide by synchrony: $F_{1,116} = 1.728$, $P = 0.191$; age: infanticide: $F_{1,68} = 0.479$, $P = 0.491$; synchrony: $F_{1,68} = 2,02$, $P = 0.160$; infanticide by synchrony: $F_{1,68} = 0.892$, $P = 0.384$; relatedness: $\chi^2_{3,65} = 6.35$, $P = 0.112$), nor in the female weight between the treatment groups (infanticide: $F_{1,67} = 1.064$, $P = 0.306$, synchrony: $F_{1,67} = 5.940$, $P = 0.482$; infanticide by synchrony: $F_{1,67} = 0.250$, $P = 0.619$).

### STATISTICAL ANALYSES

#### Weaning and breeding success

The effects of the treatments were assessed on two different aspects of female reproductive success: weaning success and breeding success. In the generalized mixed model analysis (SAS, PROC GLIMMIX with binary error distribution and log link function) on weaning success, the females' success to raise at least one young to independence was explained by infanticide and synchrony manipulations and their interaction. Enclosure was included in the model as a random effect. In the mixed models on female breeding success (the proportion of offspring successfully raised to independence, including only the females that successfully weaned at least one pup), we used the arcsine-transformed proportion of the original litter size that was successfully raised to independence (arcsine $\sqrt{proportion}$) as the response variable, and infanticide, synchrony and their interaction as fixed factors. Enclosure identity was again used as a random effect. Pairwise comparisons were performed using Tukey–Kramer option in PROC MIXED (SAS). All $P$-values are two tailed.

#### Offspring size

Individual young were used as datapoints in the analyses of weaning weights and heads, and enclosure and female identity (nested within the enclosure) were used as random effects in the mixed models. Furthermore, the number of weaned offspring was used as a covariate in the models because there was a significant negative correlation between these traits (number and weight: $r = -0.292$, $N = 192$, $P < 0.001$; number and head width: $r = -0.256$, $N = 192$, $P < 0.001$).

# Results

## WEANING SUCCESS

Because infanticide may sometimes cause a total loss of litter (Gandelman and vom Saal 1977; Brooks and Schwarzkopf 1983; Hoogland 1985, but see Elwood 1980; Wolff and Cicirello 1989) we first tested if there was a difference in the weaning success between the females in different treatment groups. We found no significant differences (infanticide: $F_{1,15.63} = 0.22$, $P = 0.644$; synchrony: $F_{1,15.63} = 1.58$, $P = 0.227$; infanticide × synchrony: $F_{1,15.63} = 2.29$, $P = 0.150$; enclosure (estimate ± SE): 0.22 ± 0.34), indicating that the total loss of litter may originate from factors other than infanticide, such as litter abandonment by mothers. Although it is possible that handling during the experiment may contribute to some litter abandonments, any such handling effect would be distributed evenly between the treatment groups. In infanticidal versus noninfanticidal populations, 47.9% and 56.9% of females, respectively, succeeded in raising some offspring to weaning. In synchronously and asynchronously breeding populations the proportions of successful females were 48.5% and 59.3%, respectively.

## BREEDING SUCCESS

The interaction between breeding synchrony and infanticide significantly explained female breeding success (Table 1), indicating that synchronous breeding affected breeding success differently between the INF and NON-INF populations. Within the NON-INF population, asynchronously breeding females had a significantly higher breeding success than synchronously breeding females (Tukey-Kramer, NON-INF/AS vs. NON-INF/S (estimate ± SE): 0.35 ± 0.12, $P = 0.034$) (Fig. 2). Within the INF population, such an advantage of asynchronous over synchronous breeding did not exist (INF/AS vs. INF/S, −0.11 ± 0.17, $P = 0.909$). Instead, among the asynchronously reproducing females, infanticide caused a significant decrease in breeding success compared to the noninfanticidal population (INF/AS vs. NON-INF/AS, 0.44 ± 0.14, $P = 0.018$), whereas among the synchronously breeding females, there was no difference in breeding success between INF and NON-INF populations (INF/S vs. NON-INF/S, −0.017 ± 0.15, $P = 0.999$). Furthermore, the main effect of infanticide

**Table 1.** Generalized linear mixed model (PROC MIXED, SAS) on female breeding success (proportion of offspring weaned to independence) in infanticide and synchrony treatments. Enclosure was included in the model as a random effect (estimate = 0, residual = 0.16).

| | df$_{num}$ | df$_{denom}$ | $F$ | $P$ |
|---|---|---|---|---|
| Infanticide | 1 | 60 | 4.18 | 0.045 |
| Synchrony | 1 | 60 | 1.31 | 0.257 |
| Infanticide × Synchrony | 1 | 60 | 4.89 | 0.031 |
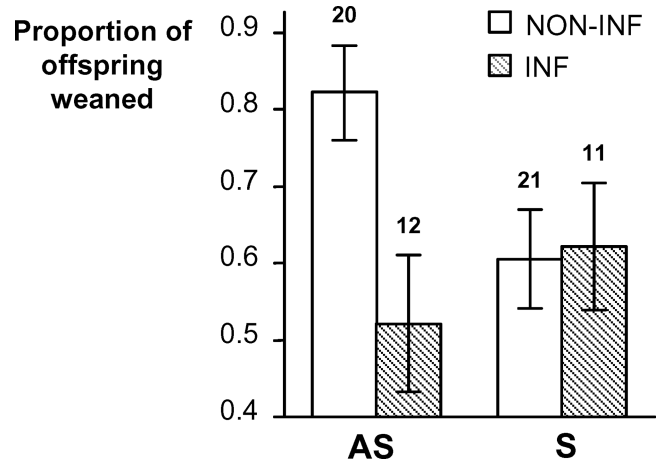


**Figure 2.** Mean breeding success of females (proportion of young weaned ± SE, including only the females that successfully weaned at least one pup) in different synchrony and infanticide groups (white bars: noninfanticidal, dashed bars: infanticidal; AS: asynchronously breeding populations, S: synchronously breeding populations). Numbers of females in each treatment group is shown above the bars.

showed that breeding success was in general higher in NON-INF than in INF populations (Table 1).

## OFFSPRING SIZE

Offspring weight at weaning differed between the infanticide treatments (Table 2), with weaned pups reaching a significantly higher weaning weight in the noninfanticidal environment. Breeding synchrony had no effect on the weaning weight of pups. Offspring head width at weaning did not differ significantly between either infanticide or synchrony treatments (Table 2).

**Table 2.** Generalized linear mixed model (PROC MIXED, SAS) on weaning weight and head width of individual pups in different synchrony and infanticide treatments. In the models, enclosure and mother (nested under enclosure) identity were used as random effects (estimate ± SE on weaning weight: mother 2.09 ± 0.62, enclosure 0.64 ± 0.58; and on weaning head: mother 0.11 ± 0.03, enclosure 0.03 ± 0.03).

| | df$_{num}$ | df$_{denom}$ | $F$ | $P$ |
|---|---|---|---|---|
| Weaning weight | | | | |
| Infanticide | 1 | 32.3 | 5.404 | 0.027 |
| Synchrony | 1 | 35.9 | 0.400 | 0.531 |
| Infanticide × Synchrony | 1 | 18.8 | 0.241 | 0.629 |
| Litter size | 1 | 53.2 | 9.425 | 0.003 |
| Weaning head width | | | | |
| Infanticide | 1 | 32.2 | 3.024 | 0.092 |
| Synchrony | 1 | 36.4 | 0.161 | 0.691 |
| Infanticide × Synchrony | 1 | 18.5 | 0.308 | 0.586 |
| Litter size | 1 | 52.4 | 5.738 | 0.020 |

# Discussion

We presented a hypothesis predicting a relationship between infanticide tactics and breeding synchrony (Fig. 1). The main findings from our experimental setup supported this hypothesis revealing the highest reproductive success in noninfanticidal, asynchronously breeding (NON-INF/AS) populations. Reproductive success was in general lower in the infanticidal (INF) populations as compared to the noninfanticidal (NON-INF) populations. Most interestingly, breeding success in the asynchronously breeding, infanticidal populations (INF/AS) was significantly lower compared to noninfanticidal populations (NON-INF/AS), whereas among synchronously breeding females, infanticide had no negative effects on breeding success (INF/S vs. NON-INF/S). These findings support the idea that synchronous reproduction could have evolved as a counterstrategy against infanticide.

## ADVANTAGE OF ASYNCHRONY

According to the hypothesis presented in the Introduction we expected an advantage of asynchronous over synchronous breeding in the noninfanticidal population. The results of our experimental setup support this prediction, showing that the highest reproductive success was reached in the NON-INF/AS population. The proportion of offspring surviving to weaning in this group was more than a third (36%) higher than in the NON-INF/S population. In terms of absolute recruit numbers (mean $\pm$ S.E), 4.1 $\pm$ 0.35 and 3.4 $\pm$ 0.42 offspring were weaned in the NON-INF/AS vs. NON-INF/S, respectively.

The proximate mechanisms mediating the benefits of asynchrony in the noninfanticidal population may be either a lower breeding density or an increased amount of food (energy) per breeder. Energy shortage can limit reproduction in some microtines, especially at the beginning and the end of the breeding season, particularly so if reproduction is synchronous causing the peak of individual energy needs simultaneously. Several studies have shown the importance of resources and lowered density on reproductive success (e.g., in rodents Ostfeld et al. 1993; Duquette and Millar 1995; Koskela et al. 1999; Prévot-Julliard et al. 1999), but there are no previous results on reproductive success in relation to reproductive synchrony in noncommunal species. Various studies indicate that increasing home range (overlapping feeding area) or territory (exclusive breeding area) size are behaviors that reduce negative density-dependent effects and increase food intake (e.g., Mares et al. 1982; Enoksson and Nilsson 1983; Kilpatrick et al. 2001; Harris and Leitner 2004). However, although asynchronous reproduction has been predicted to result in more efficient temporal space partitioning among females ensuring a greater availability of resources per breeder (Ims 1990a), in the present study offspring size at weaning did not differ between asynchronously and synchronously breeding females. Thus, although the data support the benefits of asynchrony, the current study design cannot identify the mechanisms mediating them into breeding success.

The two synchronously breeding populations (INF/S and NON-INF/S), both showed an intermediate reproductive success (proportions of offspring weaned, Fig 2). According to our hypothesis, they are facing equal costs in terms of competition for energy resources due to their synchronous reproduction and equal benefits of noninfanticidal behavior, because postpartum infanticidal females are blocked from killing pups at this time. Therefore the comparable levels of reproductive success between these two groups are consistent with the prediction of an advantage of asynchrony.

## COST OF INFANTICIDE

The experimental data verify that infanticide is an important factor affecting reproductive success. Tuomi et al. (1997) modeled the evolutionary stability of female infanticide in a simple game-theoretical context, showing that the mean fitness in a population should decrease as the frequency of infanticidal females increases. Our data show higher breeding success for females in the noninfanticidal population (mean proportion of offspring weaned in NON-INF and INF populations $\pm$ S.E: 0.71 $\pm$ 0.05 and 0.57 $\pm$ 0.06, respectively). Therefore infanticide causes a 20% decrease in offspring survival. The absolute numbers of recruits per litter show the same difference (mean $\pm$ S.E: 3.7 $\pm$ 0.28 and 2.8 $\pm$ 0.31 offspring in NON-INF and INF populations, respectively), equating to a 25% loss in recruits due to infanticide. Only a few earlier studies have tried to assess the quantitative impact of infanticide on offspring survival, but the available data indicate an even larger proportion of young killed by conspecifics. Infanticide accounted for about 30% of juvenile mortality in Belding's ground squirrels (*Spermophilus beldingi*; Sherman 1981) and 30.8–62.5% in Hanuman langurs (*Presbytis entellus*; Borries 1997). In prairie dogs (*Cynomys ludovicanus*) 51% of litters experienced total or partial infanticide (Hoogland 1985). The assessment procedures are not completely comparable with the study design here, and mortality in the absence of infanticidal individuals in the population was not determined in previous studies. Nevertheless, the potential importance of infanticide on experimental results might be considerable when dealing with infanticidal species.

Not only was breeding success higher within the NON-INF population, but offspring weight was also higher compared to INF populations. Therefore, rather than demonstrating a trade-off between the number and quality of offspring, these results suggest actual advantages for reproductive success associated with breeding within the noninfanticidal environment. Although it cannot be ascertained whether the cause of the lower reproductive success in INF populations was due to the act of infanticide per se (actual killing and harassment of the young), or some correlated character (e.g., poorer nursing ability of infanticidal females), the difference

between the infanticidal and noninfanticidal populations is evident. Because infanticide in the bank vole is a highly heritable trait (T. Mappes, J. Aspi, E. Koskela, S. Mills, T. Poikonen and J. Tuomi, unpubl. ms.), it is possible that genetically correlated traits might actually account for the result. However, there are no studies showing such genetic correlations. Further studies are needed to determine the characteristic differences (e.g., competitive abilities) between individuals representing the infanticidal and noninfanticidal tactics, with both tactics simultaneously competing in the population. Experiments should also be conducted to test whether noninfanticidal populations actively stagger their reproduction to gain advantages of asynchrony. Furthermore, in the present study, the degree of relatedness was not a manipulated variable, whereas in wild populations, polymorphism in infanticidal tendency could be expressed conditionally in relation to the identity of potential recipients (e.g., Sherman 1981; Lambin and Yoccoz 1998, but see Hoogland 1985; Wolff and Cicirello; Cicirello and Wolff 1990).

## SYNCHRONY AS A COUNTERSTRATEGY

These data demonstrate, for the first time, a relationship between the fitness effects of infanticide and synchronous breeding, suggesting that there is a connection or relationship between the two concepts. This forms a foundation for the previously proposed hypothesis (Lambin 1993; Koskela et al. 1997) that synchronous reproduction may act as a counterstrategy against offspring loss due to infanticide. Our main empirical finding in support of this hypothesis is the differential effect of infanticide on breeding success among synchronously and asynchronously reproducing females. If breeding is asynchronous, offspring survival decreases by 37% due to infanticide compared to the noninfanticidal population. In absolute numbers of recruits, this translates into $4.1 \pm 0.35$ and $2.4 \pm 0.43$ offspring in NON-INF/AS and INF/AS populations, respectively (40% lower in INF/AS population than in NON-INF/AS). If reproduction is synchronous, infanticide causes no decrease in offspring survival (3% higher offspring survival in INF/S population compared to the NON-INF/S population). Thus, reproductive synchrony acts as a counterstrategy against infanticide, because the negative effect of infanticide on mean fitness is significantly reduced in a synchronous compared to an asynchronous breeding population.

## Conclusions

The results show the negative effects of infanticide on breeding success both in the number and size of offspring raised to independence, suggesting that counterstrategies against infanticide would be adaptive. Furthermore, a decreasing advantage of asynchrony as infanticide intrudes into the population infers that reproductive synchrony could act as a counterstrategy against offspring

loss due to infanticide. The possibility that multiple strategies, for example synchronous breeding with female territoriality or aggression (e.g., Mallory and Brooks 1978; Wolff and Cicirello 1989; Wolff and Peterson 1998) can act simultaneously to prevent loss of offspring due to infanticide, is not excluded. At the same time, territoriality could also favor increased access to resources, which is also important for successful breeding.

In a boreal system, where reproduction of seasonally breeding small rodents is limited to the spring–autumn season, some degree of reproductive synchrony is inevitably expected, but increased resource availability could be beneficial enough to enhance selection toward a more staggered mode of reproduction. However, in predominantly infanticidal populations, the negative effects of infanticide on breeding success seem to be strong enough to eliminate any advantage of asynchronous reproduction. Still, not all interpretations of the study are easy to understand from an evolutionary perspective. There is strong evidence that infanticide reduces fitness and therefore it should be eliminated from the population. Why do we still observe an infanticidial tactic in natural populations, and why would it ever increase in frequency to the point that there would be selection in favor of synchronous breeding? In the present study design populations were either all noninfanticidal or all infanticidal, so the potential dynamics that could create an advantage of one phenotype over another in a polymorphic population could not be examined. Further experiments are required to determine those circumstances of competition in which an infanticidal mutant would invade noninfancidal populations. One explanation could be resource competition between breeding females as shown theoretically by Tuomi et al. (1997). The authors suggest that infanticidal females might have a competitive advantage if they are able to eliminate the offspring of neighboring females. However, survival of the noninfanticidal genotype requires a counterstrategy, either more effective offspring defense (territoriality) or greater synchronization of their timing of breeding with that of the infanticidial genotype. Additionally, small mammal population cycles (Hanski et al. 1993) coupled with the presence of generation overlap may play an important role in the maintenance of infanticide tactics. At low population density the competitive advantage for food resources is not necessarily strong enough to favor selection of an infanticidal tactic. However, at high population density when there is a strong competitive advantage for food resources, a tactic that lowers the density of competing pups, such as infanticide, would be favored. The relationship between infanticide and breeding synchronization suggests therefore, that as density increases, the advantage of synchronous breeding to offset infanticide would also increase.

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