To Breed or not to Breed: An Analysis of the Social and Density-Dependent Constraints on the Fecundity of Female Badgers (Meles meles)

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To breed or not to breed: an analysis of the social and density-dependent constraints on the fecundity of female badgers (*Meles meles*)

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CONTENTS

SUMMARY

Data from post-mortem examinations, population density estimates and long term capture–mark–recapture studies have been combined to look at the pattern of reproductive behaviour and the social factors leading to reproductive failure in badgers in Britain. The results are used to evaluate whether the hypothesis that the defence of oestrous females (as opposed to defence of food resources) best explains territorial behaviour and the social organization of badgers.

Badgers in Britain have two peaks of reproductive activity, one immediately post partum and one in the summer/autumn. These coincide with two peaks of ovulation, and in the late winter/spring there is a steep rise in the number of sows carrying blastocysts, to reach an asymptote in June for yearling sows and April in older sows. Measured by their contribution to overall productivity, winter/spring matings were much more important than summer/autumn matings, contributing 65% of total autumn blastocysts in yearling sows and 71% of autumn blastocysts in older sows. The relative importance of the two mating periods is reflected in the seasonal pattern of bite wounding in adult male badgers; minor bite wounding in January–March was 2.3 times as frequent as in August–October, and moderate–extensive bite wounding was 3.1 times more frequent.

In the populations studied, pre- and post-natal losses were high, with reproductive failure occurring at all stages of the breeding cycle, so that less than 30% of potential productivity was achieved. Indeed 22% of sows failed to develop blastocysts; these had a lower body mass, less body fat, larger adrenal glands, poorer health and higher bite wound scores than sows with blastocysts. Only 44% of adult sows implanted their blastocysts and proceeded to the end of pregnancy. However, it was less easy to identify features characteristic of sows that did or did not go on to implant their blastocysts. Finally, 35% of sows

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that produced cubs ceased lactation early, and this loss of entire litters was thought to be due to infanticide by dominant sows. The presence of annexe setts correlates with increased productivity in younger sows, and this is thought to be because annexe setts enable younger sows and their cubs to avoid the aggression of older, more dominant sows.

Living in large social groups has no net reproductive gain for adult males or females, and there was a decline in productivity (per adult) with increasing group size. Although paternity measures were not available to assess the individual gains from group living, the absence of mate guarding and the frequency of cuckoldry and of mixed-paternity litters suggests that mating is not the sole, or probably even the major, prerogative of a dominant boar. The data so far question the hypothesis that the social organization of badgers evolved to monopolize access to oestrous females.

1. INTRODUCTION

Ever since Fries (1880) described unimplanted blastocysts in female badgers (*Meles meles*) killed during the summer and autumn, studies on badger reproduction have mainly been concerned with the phenomenon of delayed implantation. These studies have either been descriptive, documenting the process (see, for example, Harrison & Neal 1956; Neal & Harrison 1958; Harrison 1963; Ahnlund 1980; Wandeler & Graf 1982; Whelan & Hayden 1992), or physiological, in particular trying to understand the hormonal factors regulating the process (see, for example, Canivenc & Bonnin-Laffargue 1963; Canivenc 1966; Canivenc & Bonnin 1975, 1979, 1981; Canivenc *et al.* 1981*a*,*b*; Mondain-Monval *et al.* 1983; Maurel *et al.* 1984).

In general, although a very small proportion of female badgers may breed in the autumn of their first year (Fargher & Morris 1975; Ahnlund 1980), most do not ovulate until the spring or early summer of their second year (Wandeler & Graf 1982). Thereafter the majority of sows ovulate and develop blastocysts each spring, and the proportion of sows with unimplanted blastocysts remains constant until the end of the year. Based on the work of Ahnlund (1980) in Sweden, the following summary can be drawn. For male badgers, testis mass reaches a peak in February–March, and then declines slowly until October–November; the proportion of animals with spermatozoa present in the testes declines from August onwards, although some animals possess sperm until October. However, Graf & Wandeler (1982) reported that in Switzerland badgers with a high concentration of spermatozoa in the tubuli of their epididymides occur throughout the year. The pattern of testicular size described by Ahnlund (1980) probably coincides with the pattern of mating behaviour; there is a peak in reproductive activity post partum, with most sows other than yearlings having ovulated by March or April, and 50% are pregnant by the end of March, with 90–95% pregnant by June. Thereafter there is no significant change in the number of pregnant sows, although further ovulations occur in pregnant animals until August. The number of ova shed during late ovulations may be smaller than early in the season, perhaps reflecting the decreasing fertility of males from August onwards.

Although the pattern of mating activity in wild badgers is not well documented (Harris *et al.* 1990), there is believed to be a spring peak, with mating occurring until December, perhaps with a smaller autumnal peak (Neal 1986). Spring matings are said to be of long duration, autumn matings of shorter duration (Paget & Middleton 1974; Neal 1977). The long duration of mating has led Ahnlund (1980) to argue that badgers are induced ovulators, a view supported by Canivenc (1966).

Although matings and ovulations occur throughout the spring and summer, Ahnlund (1980) concluded that the replacement or addition of blastocysts in pregnant badgers is a rare event. He suggested, therefore, that repeated ovulations may have become more important as a factor in the social organization of badgers. In particular, because sows may mate with several boars during an oestrus (Neal & Harrison 1958; Paget & Middleton 1974; Neal 1977), it may be a means of maintaining group cohesion, as claimed in a variety of other mammals.

However, there is little evidence to support such an argument. Although studies in Britain (Kruuk 1978; Cheeseman *et al.* 1981; Harris 1982) have characterized badgers as social animals, with only a low level of intergroup movements and preferential recruitment of young born into the group (Cheeseman *et al.* 1988), close inbreeding is offset by delayed dispersal, with adults sometimes transferring permanently between groups, and by mating occurring between males of one group and females of another (Evans *et al.* 1989). This is an unusual mating system among mammals, and may not be the pattern for much of the badger's range (from Ireland to Japan), as in many habitats the species is largely solitary or only forms pairs (Kruuk 1989). Whether the species is territorial in such situations is unclear. Large social groups with small territories appear to be particularly associated with productive agricultural habitats such as those found in Britain, where 97% of the badger population is found in managed landscapes (Reason *et al.* 1993). It may be, therefore, that group living in small, well-defined territories is a relatively recent adaptation to man-induced changes in the habitat, and that the high-density badger populations seen in southern England are a recent phenomenon (Cresswell *et al.* 1989).

Just how common group living is throughout the badger's range is at present unknown, but it is clearly one end of a spectrum of social patterns (Neal 1986; Kruuk 1989). The ecological factors leading to strict territorial defence and group living by badgers in Britain were studied by Kruuk & Parish (1982), who explained these phenomena in terms of defending a food resource. In particular they argued that the distribution of areas rich in earthworms (*Lumbricus* spp.) is correlated with badger range size, whereas badger group size increases with the biomass of earthworms per badger territory, and badger density increases with overall earthworm biomass. They concluded that the regulation of badger density is likely to take place through the regulation of group size, and that by this means badger populations are adjusted to food availability. Kruuk & Parish (1987) suggested that when food availability is low, the badger's spatial organization may revert to solitary, single-sex ranges, as found in the majority of mustelids.

More recently, whether this is the sole, or even the major, factor leading to territoriality in badgers has been questioned by Roper *et al.* (1986). They showed that the pattern of territorial scent marking with faeces (the use of latrines) is bimodal, with a large spring peak, which they believed is associated with the spring mating period, and an autumn peak, which they suggested is associated with an upsurge in mating behaviour. Roper *et al.* (1986) argued that territoriality is a mechanism for discouraging kleptogamy in badgers, and that territorial males are attempting to prevent neighbours gaining reproductive access to resident females. Davies *et al.* (1987) presented evidence that there is also a bimodal pattern of road-traffic mortality for both sexes, which they suggested reflects an underlying bimodal pattern of mating behaviour. At present there is no convincing evidence for bimodality in the reproductive behaviour of badgers, although it is clearly difficult to explain an autumn peak of latrine use in terms of food defence, especially when summer (a period of reduced latrine use) is the time when food is often shortest, and in dry summers (when food availability is limited) cub mortality can be very high (Cheeseman *et al.* 1987).

Although the factors leading to the evolution of territoriality and group living in badgers are the subject of debate, some of the consequences in terms of reproductive success are known. In Sweden, Ahnlund (1980) found that approximately 50% of yearling sows and 90–95% of older sows developed blastocysts, and that during the course of the winter there was no diminution in the number of pregnant sows, i.e. most, if not all, of these sows went on to implant their blastocysts. In Britain, the limited data available (reviewed by Anderson & Trewhella 1985) suggest that there is a considerable reduction in the number of sows that actually implant their blastocysts and proceed to parturition. These data are supported by long-term capture–mark–recapture studies (Cheeseman *et al.* 1987; Harris & Cresswell 1987), where only a minority of sows in their second to fourth years bred each year. In addition, these authors estimated that there is a considerable loss of cubs (average for the two studies of 38%) pre-emergence, and that this loss is probably in large part due to infanticide and other social factors (Lüps & Roper 1990; Harris *et al.* 1992*a*). Clearly, the social organization of badgers in Britain leads to a significant loss of reproductive potential. However, population perturbations leading to the disruption of group structure can have a dramatic effect in inhibiting reproduction, and it appears that in normally high-density populations a degree of stability in social organization and group structure is necessary for successful breeding (Anderson & Trewhella 1985; Cheeseman *et al.* 1992). How these observations equate with the fact that in low-density populations badgers do not form social groups but breed successfully is unclear.

When reviewing the literature on badger population dynamics, Anderson & Trewhella (1985) concluded that long-term population stability arose as a consequence of density-dependent constraints on fecundity, and that such constraints only operate at densities close to the carrying capacity of the habitat. However, the mechanisms by which fecundity or the high levels of early cub mortality are influenced by density are not well understood. Neal (1977) argued that stress on females induced by frequent contact in high-density populations is important, and Kruuk (1978) suggested that social status may be important, with typically only one litter produced per social group. Whether this is the norm is unclear; long-term capture–mark–recapture studies on the two high-density populations described in this study showed that 35% of social groups fail to breed each year, 45% produced one litter of cubs, 15% two litters, 5% three litters and $<1\%$ four litters ($n = 337$) (C. L. Cheeseman & S. Harris, unpublished results). In general, however, Anderson & Trewhella (1985) concluded that no quantitative evidence of any association between fecundity and population density was available, and they suggested that a manipulative field study should be undertaken to confirm or refute their assumption that badger fecundity is density dependent.

Although the basic reproductive pattern for badgers is understood, many of the details are unclear or are the subject of speculation. Therefore this paper aims to address the following questions: (i) is the pattern of badger reproductive behaviour in Britain bimodal? (ii) If so, what are the relative contributions of the two peaks in mating to overall fecundity? (iii) What features characterize breeding as opposed to non-breeding sows? (iv) Is reproductive success related to status, and how does the reproductive performance of individual animals vary from year to year? (v) How does population density affect fecundity, and what, if any, are the principal density-dependent effects on population growth? (vi) Whether monopolizing access to oestrous females best explains the territorial and reproductive behaviour of badgers in Britain.

2. METHODS

(*a*) *Post-mortem studies*

Between March 1988 and March 1990, 352 adult female and 298 adult male badgers were collected from Avon, Devon, Dorset, Gloucestershire and Wiltshire. Of these 650 badgers, 56.3% were killed on the roads and 41.7% deliberately culled by the Ministry of Agriculture, Fisheries and Food (MAFF) as part of their bovine tuberculosis control scheme; the remainder died from a variety of causes. For this

Table 1. *The main and annexe sett density classes used in the analyses; density was measured as the number of setts per square kilometre*

main sett density		< 0.40		0.41–0.45		0.46–0.50		> 0.51
land classes		4,8		1,2		6,7		5
annexe sett density	< 0.10		0.11–0.15	0.16–0.20	0.21–0.25		0.26–0.30	0.31–0.35
land classes	4,8		—	1	2,7		6	5

paper, each year class starts on January 1, and animals are defined as adult from January 1 of the year following their birth. For some analyses adults are divided into yearlings and animals ⩾3 years old; the former are animals killed between January 1 and December 31 of the year following their birth, and the latter are animals killed on or after January 1 of the following year. Where analyses are undertaken by seasons, spring is defined as March–May, summer June–August, autumn September–November and winter December–February.

Each carcass, excluding any animals that had lost a significant amount of fluid or tissue, was weighed to the nearest 0.1 kg. All carcasses were then examined for bite wounds on four regions (head, neck, rump, elsewhere) and for each region bite wounds were classified on a 1–6 scale as follows: 1 = none, 2 = healed minor, 3 = fresh minor, 4 = fresh moderate, 5 = healed extensive and 6 = fresh extensive. These were then summed to give a cumulative body bite wound count on a scale of 4–24. On dissection the extent of omental fat was estimated by the proportion of the viscera that were obscured, such that 1 = 0–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80% and 5 = 81–100%. A similar measure (on a 1–5 scale) was also obtained for the fat cover in the pelvic region and around the kidneys.

Both adrenal glands were removed, fixed in 10% formal saline and later air dried and weighed. During the post-mortem, any indications of infection (tuberculosis or otherwise), emaciation, or substantial tissue damage were noted, and tissue samples were taken by MAFF for culture for *Mycobacterium bovis*. These results were used to calculate a health score as follows: 1 = healthy, 2 = tuberculosis on culture only, 3 = minor infection with tuberculosis or other unidentified disease, 4 = substantial infection with tuberculosis or other unidentified disease, and 5 = emaciation, chronic tuberculosis and emaciation, chronic unidentified infection or significant tissue damage following infection or earlier trauma.

For sows, the reproductive tract was removed intact from below the cervix, with the vagina securely closed with suture thread, and stored chilled in buffered saline. Subsequently each horn of the uterus was split and the positions of any blastocysts noted. These were then flushed out and retained. The elutant was carefully checked for errant blastocysts. As these were relatively easy to locate, few if any would have been missed. Each blastocyst was then flattened under a gridded coverslip and its diameter measured to the nearest 0.1 mm. The position, size, colour and description of any placental scars were recorded, and any fetuses were counted, removed, weighed and their crown-rump lengths recorded. The overall appearance of the uterine wall was also recorded.

The ovaries were then removed from their bursae and the diameter of any corpora lutea and large pre-ovulatory or atretic follicles were measured to the nearest 0.1 mm. An approximate count of the number of primordial or small atretic follicles (< 0.05 mm) was also made, and the ovaries then weighed. The development of the nipples was used to assess whether the sow had suckled cubs in the past, and an excised section of mammary tissue was examined to determine whether the animal was lactating.

(*b*) *Age determination*

Unlike in some other parts of its range (Ahnlund 1976; Grue & Jensen 1979), no clear annual incremental lines could be distinguished in the teeth of badgers from South-west England (Fargher & Morris 1975; present study), and so an alternative method of age determination had to be used. For each animal, the head and a fore foot (removed by cutting through the radius and ulna below the elbow) were stored in formal saline. Animals up to 18 months old were aged by the degree of epiphyseal fusion in the fore foot; the distal epiphyses of the radius and ulna were the last to close (Fargher & Morris 1975). Thereafter animals were aged to year classes using tooth wear, with animals ⩾7 years combined. Despite controversy over the use of this technique (Hancox 1988; da Silva & Macdonald 1989), by reference to the date of death and comparison with a sample of known-age badgers, trials showed that up to 74% of the animals could be assigned to the correct year class, and up to 98% ± 1 year (Harris *et al.* 1992*b*). This level of accuracy was deemed adequate for the present analysis.

(*c*) *Estimating population density*

To determine the population density for the area from which each carcass had been collected, the results from a recent national badger census were used (Cresswell *et al.* 1990). This survey was stratified using the land classification scheme developed by the Institute of Terrestrial Ecology (Bunce *et al.* 1981*a*,*b*). For this, map-derived variables were used to allocate selected 1 km squares on a grid to one of 32 land classes. Of these squares, 2455 were surveyed for badgers between November 1985 and January 1988, and the mean badger density (social groups per square kilometre) calculated for each land class. Full details of the methodology are given in Cresswell *et al.* (1990).

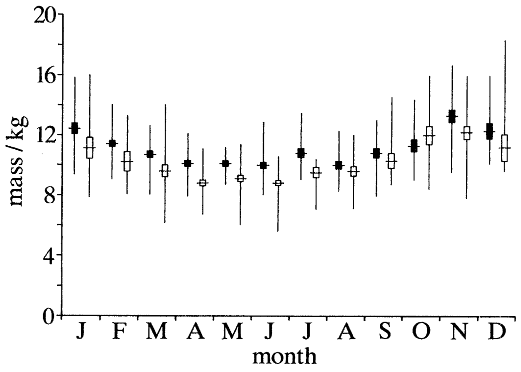

Figure 1. Monthly whole mass changes in adult badgers, showing the mean, s.e. and range of measurements; boars (filled rectangles), sows (open rectangles).

Subsequent improvements to the land classification scheme (R. G. H. Bunce, unpublished results) have meant that some squares have been re-allocated to a new land class, thereby removing some of the variability within a land class, and every 1 km square in Britain has now been allocated to a land class. Using the new classification, mean badger densities have been re-calculated for each land class (Reason *et al.* 1993); the population density ascribed to each carcass was this new mean estimate for the land class from which the animal was recovered. The carcasses were all recovered from seven land classes and for the analysis these were separated into four groups by main sett density and six groups by annexe sett density (table 1). Descriptions of these sett types are given in Cresswell *et al.* (1990).

(*d*) *Long-term demographic data*

Long-term capture–mark–recapture studies were undertaken at two sites in two of the same counties from which the post-mortem material was collected. One site is in Gloucestershire; see Cheeseman *et al.* (1981, 1985) for a description of the study site. The other is in Avon in the suburbs of Bristol; see Harris (1982, 1984) for a description of the study site. At both locations animals were caught by using cage traps, snares or hand-held nets, weighed, the breeding condition of sows recorded, any signs of disease noted, and new animals marked with a combination of ear tags and inguinal tattoos (Cheeseman & Harris 1982). The majority of animals were caught each year, and as most animals were first caught and marked as cubs, or a few as yearlings, they were predominantly of known age and of known natal group (Cheeseman *et al.* 1987; Harris & Cresswell 1987). Population estimates were obtained from the capture records by direct enumeration. This includes all animals caught on a particular occasion, plus those marked previously that were not caught that year but which reappeared during a subsequent trapping session. In the case of a badger first caught as an adult, that badger was assumed to have been present in the same social group the previous year. The method of direct enumeration assumes little movement in the population, which was the case in both studies (Cheeseman *et al.* 1988).

Trapping operations at the Gloucestershire site commenced in 1976, at the Bristol site in 1978. These continue at the Gloucestershire site, whereas extensive trapping operations at Bristol were discontinued in 1988. The long-term demographic data from these two studies were used to investigate the reproductive performance of individual sows and to see if there is any association between group size and breeding success.

3. RESULTS

(*a*) *Seasonal changes in body condition*

Many of the measurements used in the post-mortem work as indicators of an animal's condition were both seasonally variable and showed different patterns of variability between the sexes. When comparing whole mass changes in adult males and females (figure 1), whilst the overall pattern was similar, the over-winter masses of females were considerably more variable, and they declined more in the summer. Females also exhibited considerable variation in fat estimates throughout the year (figure 2), with minimum values from June to September. In contrast, males showed no summer decline but possibly had a trend towards higher values in December and January.

Bite wounding in males followed a roughly bimodal pattern, with one distinct peak in February–March and a less well defined increase around September. The incidence of moderate–extensive wounding mirrored the overall pattern (figure 3). There was no correlation between bite wounding in males and either body mass ($r = 0.0154$, $p > 0.05$) or adrenal weight ($r = 0.1321$, $p > 0.05$). The pattern in females, how-

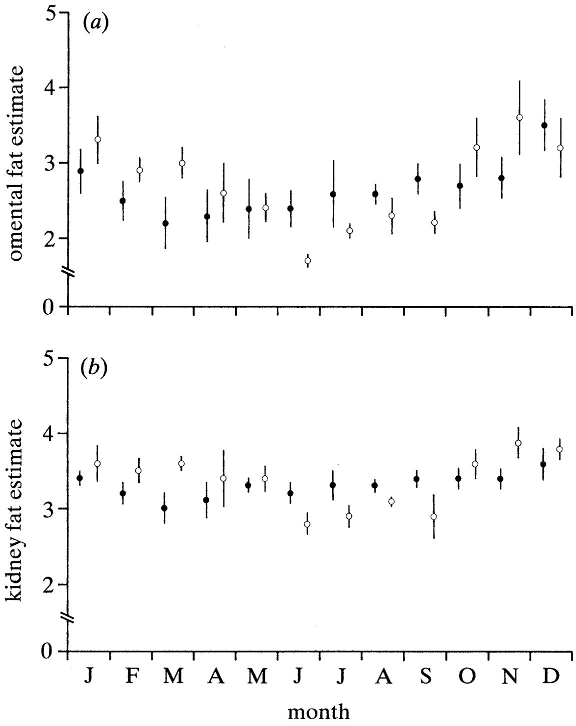

Figure 2. Monthly fat changes in adult badgers. (*a*) Omental fat, (*b*) kidney fat. The figures are means ± s.e.; boars (filled symbols), sows (open symbols).

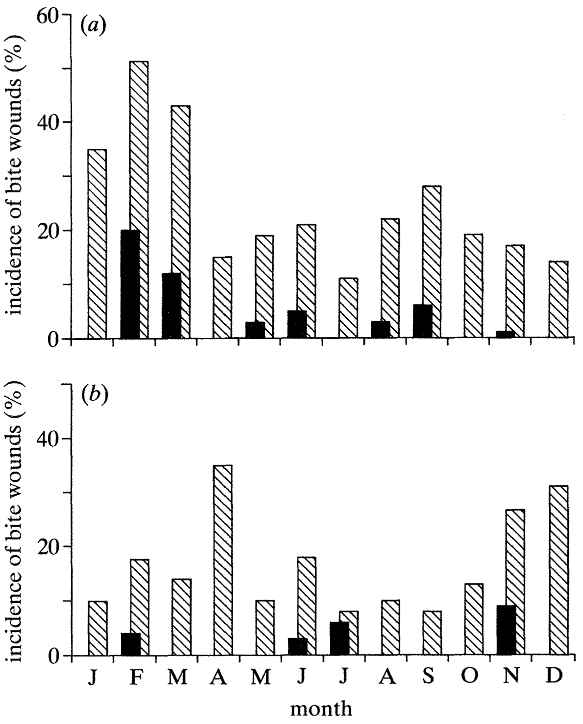

Figure 3. Monthly changes in the incidence of bite wounding in adult badgers. (*a*) Boars, (*b*) sows. Hatched columns show minor wounds, solid columns show moderate–extensive wounds as described in text.

ever, was different. The overall incidence of bite wounding was lower, the peaks were less well defined, and in contrast to males occurred in April and November–December. Moderate–extensive wounding was rare in females and sporadic throughout the year.

(*b*) ***The seasonal reproductive pattern***

Figure 4 shows the percentage of females in different age classes which carried large pre-ovulatory follicles in each month of the year. For females $\geqslant 3$ years old there was a seasonal pattern similar to that for bite wounding in males, with peaks in January–February and July–September. Yearling females first came into reproductive condition later than adult sows (March–April), but the peaks coincided later in the year.

By the end of March blastocysts were recorded in approximately 80% of all adult females (figure 5). By comparing the numbers of adult females with/without blastocysts and those with/without corpora lutea from April to November (figure 6), of the 22% of adult sows without blastocysts, 9% did not ovulate and 13% ovulated but were not fertilized. During the summer the mean number of blastocysts per pregnant female fell from 3.7 in March to 2.6 in June–July (figure 7). This increased slightly from September to November, probably as a result of some yearling females coming onto oestrus for the first time and older females ovulating a second time. This is supported by the ratios of corpora lutea to blastocysts in each month (figure 8); these show that some blastocysts were lost during the summer, and then again from October onwards.

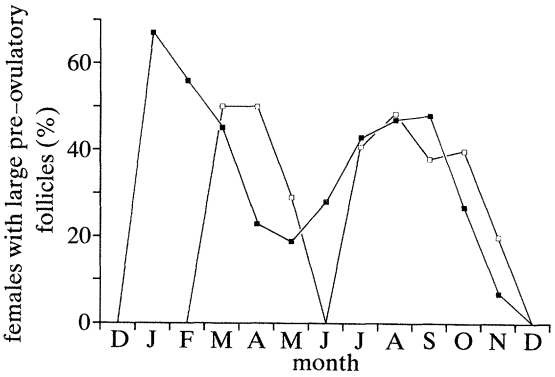

Figure 4. Seasonal occurrence of large (> 1.0 mm) pre-ovulatory follicles in female badgers. Sows $\geqslant 3$ years old (filled symbols), yearling sows (open symbols).

(*c*) ***Characteristics of sows with and without blastocysts***

The age distributions of sows $\geqslant 3$ years old with and without blastocysts are given in table 2; there was no significant difference in the age structure of the two sub-populations ($\chi^2 = 2.12$, $p > 0.05$). To look at the features which characterized the sub-population of females without blastocysts, multivariate *t*-tests were used to compare the various body condition measures for animals with/without blastocysts; each test was performed separately for each quarter of the year to control for the seasonal changes in some of the condition variables. Sows without blastocysts were characterized by lower scores for body fat, lower body mass, larger adrenal glands, poorer health and a higher bite-wound score (table 3). With the multivariate analysis of variance, highly significant differences were observed between the two groups of females in each quarter, and using discriminant analysis 88%, 73% and 77% (spring, summer and autumn) of sows were correctly classified as with/without blastocysts. Misclassification rates were confirmed using split-sample and cross-validation techniques; all were within 5%.

(*d*) ***Winter/spring against summer/autumn matings***

Plotting blastocyst sizes in each month (figure 9) showed that they grew slowly at a fairly constant rate

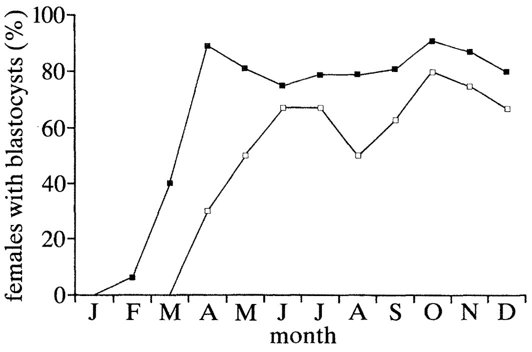

Figure 5. Seasonal occurrence of blastocysts in female badgers. Sows $\geqslant 3$ years old (filled symbols), yearling sows (open symbols).

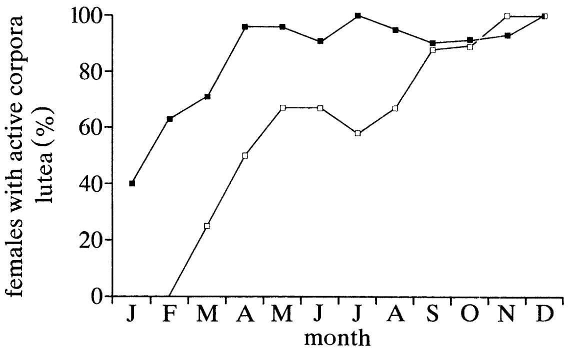

Figure 6. Seasonal occurrence of active corpora lutea in female badgers. For January to March these figures exclude any corpora lutea from the previous pregnancy. Sows ⩾3 years old (filled symbols), yearlings sows (open symbols).

during the period of diapause. However, as figure 9 shows, there was a second cohort of smaller blastocysts arising from the second peak in ovulations from mid-August onwards. Of the 20 females carrying second cohort blastocysts, six were yearlings and these had a similar corpus luteum: blastocyst ratio, three were animals ⩾3 years old with approximately twice as many corpora lutea as blastocysts, and with the blastocysts all of a similar size, whilst 11 other animals ⩾3 years old had a similar corpus luteum: blastocyst ratio but with two distinct size groups of blastocysts. Thus of the adult females, it would appear that the first group were either not fertilized in the winter/spring, or had subsequently lost their blastocysts, whilst the latter group had come into oestrus and been fertilized in the summer/autumn whilst already pregnant from winter/spring matings. Of the adult sows, females exhibiting super-fetation accounted for 21% of the sample of sows ⩾3 years old collected between September and December (and 25% of those sows ⩾3 years old with blastocysts), and the three sows with only small, summer/autumn blastocysts constituted 7% of the sample of sows ⩾3 years old collected between September and December. As no sows ⩾3 years old were recorded with only small, summer/autumn blastocysts and an equivalent corpora lutea: blastocyst ratio, it seems that few sows ⩾3 years old ever delay ovulation until late summer/autumn. Of the 20 yearlings with blastocysts collected September to December, 14 (70%) were fertilized in the winter/spring, and 6 (30%) in the summer/autumn.

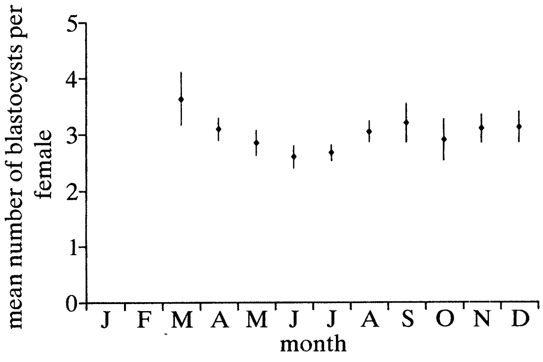

Figure 7. Seasonal changes in the mean number of blastocysts per adult sow. Figures are means + s.e.

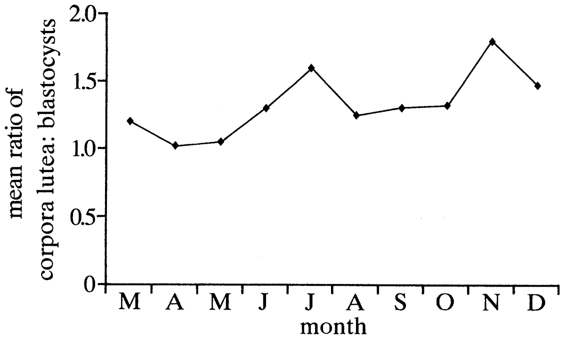

Figure 8. Seasonal changes in the mean ratio of corpora lutea: blastocysts in adult sows.

(*e*) *Characteristics of sows that do and do not produce cubs*

Sows which actually produced cubs were identified as those having fresh placental scars, signs of lactation, or obviously enlarged nipples that had recently been sucked. Age was found to have a considerable effect on breeding success (table 4), with few sows breeding before their fourth year. Applying the figures in table 4 to the total number of females in each year class, 44% of adult females produce cubs each year.

To examine the effects of body condition on whether or not an individual sow produces cubs, all adult females with/without fresh placental scars were compared using a series of multivariate *t*-tests. However, it was considerably more difficult to distinguish those females that do/do not produce cubs than animals with/without blastocysts. Using the multivariate test, the only significant result was for the spring sample (table 5), where females with fresh placental scars had significantly lower body mass and fat scores. There were occasional significant univariate relations suggesting that lower health scores (i.e. healthier) and small adrenal glands were typical of some breeding females. Not surprisingly, a discriminant analysis was unsuccessful in distinguishing females that do/do not produce cubs; 59%, 71%, 41% and 49% were correctly classified in winter, spring, summer and autumn, respectively. Misclassification rates were confirmed using split-sample and cross-validation tech-

Table 2. *Age distribution of females ⩾3 years old with and without blastocysts from April to December*

	without blastocysts		with blastocysts	
	n	%	*n*	%
3rd year	10	29.4	38	23.6
4th year	7	20.6	30	18.6
5th year	6	17.6	20	12.4
6th year	2	5.9	14	8.7
7th+ year	9	26.5	59	36.6
total	34		161	

Table 3. *Characteristics of sows with/without blastocysts; figures are means ± s.e.*

	spring (April and May only)	summer (June–August)	autumn (September–November)
Hotellings t^2-multivariate test of significance	0.7683 $p < 0.001$	0.5773 $p < 0.001$	0.2110 $p < 0.01$
health			
with blastocysts	1.51 ± 0.06	1.35 ± 0.05	1.21 ± 0.09
without blastocysts	2.80 ± 0.49	2.84 ± 0.53	2.22 ± 0.67
significance of univariate F	$p < 0.001$	$p < 0.001$	$p < 0.05$
bite wounds			
with blastocysts	5.76 ± 0.23	4.68 ± 0.24	4.36 ± 0.14
without blastocysts	9.17 ± 0.81	6.36 ± 0.94	4.78 ± 0.52
significance of univariate F	$p < 0.001$	n.s.	n.s.
adrenal mass			
with blastocysts	0.44 ± 0.03	0.42 ± 0.01	0.39 ± 0.02
without blastocysts	0.76 ± 0.06	0.69 ± 0.05	0.49 ± 0.04
significance of univariate F	$p < 0.001$	$p < 0.001$	$p < 0.05$
omental fat			
with blastocysts	2.50 ± 0.12	2.15 ± 0.09	3.10 ± 0.11
without blastocysts	1.55 ± 0.29	1.61 ± 0.26	1.89 ± 0.59
significance of univariate F	$p < 0.001$	$p < 0.01$	$p < 0.01$
kidney fat			
with blastocysts	3.45 ± 0.12	2.89 ± 0.09	3.56 ± 0.09
without blastocysts	2.66 ± 0.45	2.18 ± 0.29	3.01 ± 0.46
significance of univariate F	$p < 0.05$	$p < 0.01$	n.s.
whole body mass			
with blastocysts	8.92 ± 0.16	9.39 ± 0.12	11.71 ± 0.27
without blastocyts	7.90 ± 0.42	9.16 ± 0.27	8.83 ± 0.57
significance of univariate F	$p < 0.01$	n.s.	$p < 0.001$

niques; all were within 5% (spring, summer and autumn results were within 1%).

In addition to the sows that failed to implant, during March and April 9 out of 26 (35%) of sows that did produce cubs had ceased to lactate, before the cubs could have been weaned. The ages of the sows that stopped lactation, and hence had presumably lost their entire litter post partum, are given in table 6.

(*f*) ***Density-dependent effects on breeding success***

From the post-mortem data, an analysis of variance showed that there were no significant differences in age structure among land classes or density classes, nor was there any difference in the proportion of adult females with placental scars from the different land classes, or main sett density classes, using a χ^2 test of trends in proportions (Armitage & Berry 1987). However, there was a significant trend in the proportion of sows breeding in the different annexe sett density classes ($\chi^2 = 11.00, p < 0.05$) (table 7). This was a function of the number of younger sows whose blastocysts implant, rather than an increased proportion of sows carrying blastocysts or an increased litter size. When third year animals, which included those with signs of having bred as yearlings, were removed from the analysis, the trend was no longer significant ($\chi^2 = 3.77, p > 0.05$). None the less, the trend was still apparent, and there remained a significant difference between the lowest and highest density classes ($t = 2.03, p < 0.05$). This difference was no longer present when fourth year animals were removed. Population density appeared to have no significant effect on body condition; there were no significant differences in health scores, bite wounds, body mass, fat scores or adrenal mass between main or annexe sett density classes (table 8).

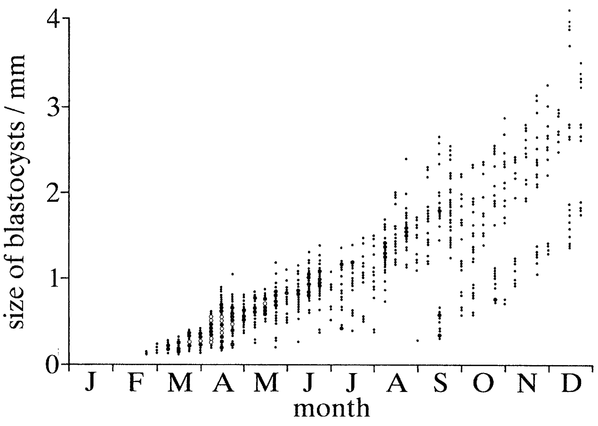

Figure 9. Seasonal changes in the size of blastocysts. Small filled circles denote single blastocysts, large filled circles 2–5 blastocysts, open circles 6+ blastocysts.

(*g*) ***Effects of social group size on productivity***

The effects of varying group size on productivity in the two populations are summarized in tables 9–12. Because the same social group will appear in different categories in different years, the data are not indepen-

Table 4. *Effects of age on breeding success of sows*

(The figures show the proportion of each age class with fresh placental scars or other signs of having produced cubs at the start of that year class (and therefore ovulated and were fertilized in the previous year))

	n	animals believed to have bred (%)
2nd year	69	0
3rd year	61	20
4th year	49	35
5th year	39	61
6th year	34	76
7th+ year	83	83

dent and are used simply to show trends rather than treated to detailed analysis. Although group size tended to be larger in the Gloucestershire population, the pattern was similar in both populations. With an increasing number of males ⩾3 years old per social group, there is a declining sex ratio (females per male), no significant effect on the number of cubs produced per social group (in Gloucestershire; the situation in Bristol was less clear because of the very small number of groups with several males ⩾3 years old), and a steady decline in the number of cubs produced per adult male and adult female. For groups containing more sows ⩾3 years old, there is an increasingly skewed sex ratio in favour of females, an increase in the number of cubs produced per social group, a steady decline in the number of cubs produced per sow and no discernible trend in the number of cubs produced per boar.

4. DISCUSSION

These studies on badger reproduction were undertaken in South-west England in an area of high badger density (Cresswell *et al.* 1990), and the population density recorded at the long-term Gloucestershire study site is the highest so far recorded anywhere (Neal & Cheeseman 1991). The post-mortem material was collected from seven land classes, and in these mean badger densities (±s.e.) ranged from 0.169±0.049 (land class 4) to 0.646±0.135 (land class 5) social groups km^{-2}; 81% of the total British badger population lives within this range of densities (Reason *et al.* 1993). However, in much of their range outside Britain badgers live at lower densities than these; see Griffiths (1991) for a review of badger numbers in the rest of Europe west of Russia. Hence the data presented here represent the pattern seen at the upper end of a range of population densities and patterns of social organization, although the data are likely to be typical of a significant proportion of the British badger population. The area chosen is also likely to show the most extreme example of social and

Table 5. *Characteristics of sows with/without fetuses or placental scars; figures are means ± s.e.*

	winter (February only)	spring (March–May)	summer (June–August)	autumn (September–November)
Hotellings t^2-multivariate test of significance	0.0839 n.s.	0.1313 $p < 0.01$	0.0533 n.s.	0.0710 n.s.
health				
with blastocysts	1.42±0.13	1.35±0.09	1.41±0.12	1.34±0.08
without blastocysts	1.79±0.17	1.71±0.19	1.38±0.13	1.39±0.16
significance of univariate *F*	$p < 0.05$	$p < 0.05$	n.s.	n.s.
bite wounds				
with blastocysts	5.33±0.51	5.90±0.31	4.79±0.24	4.40±0.15
without blastocysts	4.98±0.63	5.73±0.37	4.69±0.24	4.42±0.21
significance of univariate *F*	n.s.	n.s.	n.s.	n.s.
adrenal mass				
with blastocysts	0.35±0.03	0.32±0.02	0.41±0.01	0.33±0.01
without blastocysts	0.56±0.07	0.46±0.05	0.43±0.02	0.48±0.04
significance of univariate *F*	$p < 0.05$	$p < 0.05$	n.s.	$p < 0.05$
omental fat				
with blastocysts	3.13±0.18	1.91±0.09	2.02±0.11	2.94±0.10
without blastocysts	3.09±0.25	2.44±0.16	2.11±0.13	2.85±0.13
significance of univariate *F*	n.s.	$p < 0.05$	n.s.	n.s.
kidney fat				
with blastocysts	3.78±0.22	3.34±0.14	2.89±0.08	3.53±0.07
without blastocysts	3.62±0.20	3.59±0.13	2.87±0.12	3.49±0.12
significance of univariate *F*	n.s.	n.s.	n.s.	n.s.
whole body mass				
with blastocysts	10.40±0.32	8.76±0.22	9.32±0.23	11.76±0.30
without blastocysts	10.00±0.69	9.46±0.15	9.27±0.16	11.01±0.51
significance of univariate *F*	n.s.	$p < 0.05$	n.s.	n.s.

Table 6. *Age distribution of females in March and April that had stopped lactation early (i.e. lost their entire litter of cubs) and those that were lactating or had completed lactation*

	stopped lactation early		lactating or completed lactation	
	n	%	*n*	%
3rd year	3	33.3	5	12.2
4th year	1	11.1	3	7.3
5th year	1	11.1	7	17.1
6th year	1	11.1	9	22.0
7th+ year	3	33.3	17	41.5
total	9		41	

density-dependent constraints on the fecundity of female badgers; hence its selection for this study.

From this analysis it is clear that badgers do have two peaks of reproductive activity, one immediately post partum in the winter/spring and one in the summer/autumn. Coincidental with this are two winter/spring peaks of ovulation, one by animals ⩾3 years old and the other by yearling sows. These probably reflect the double peak in long-duration spring matings in February and April/May recorded by Neal (1986). Canivenc (1966) thought that renewed ovulations in badgers were not common, whereas Neal & Harrison (1958) and Harrison (1963) thought that there were several ovulations a year, although Harrison (1963) concluded that ova from secondary ovulations were probably lost. Ahnlund (1980) also concluded that, in Swedish badgers at least, comparatively few animals display renewed ovulations, and that the replacement or addition of blastocysts during the period of delayed implantation is a rare event, whereas Wandeler & Graf (1982) suggested that at least some of the ova shed during delayed implantation are fertilized. The data from the present study show that, at least in the high-density population studied, summer/autumn ovulations are the norm (virtually all sows have pre-ovulatory follicles; figure 4). Whilst no sows ⩾3 years old delayed ovulation until the summer/autumn, 7% of sows of this age collected from September to December had lost their spring blastocysts and became pregnant again in the autumn, and 21% more showed super-fetation.

Previous authors have been unsure about the periodicity of oestrous cycles, or the frequency or pattern of matings in badgers. Based on observations of wild badgers, Paget & Middleton (1974) suggested that badgers have an oestrous cycle of 30–40 d. From the statements given by earlier authors, most had surmised that badgers have a series of oestrous cycles throughout the summer, into the early autumn. In this study there was no evidence for an increase in the number of blastocysts per sow except in the winter/spring and summer/autumn (and in fact in between there is a gradual decline; figure 7). Because it is unlikely that an oestrus will occur in the absence of ovulation, these observations suggest that sows have a series of winter/spring oestrous cycles until they become pregnant, and thereafter have a summer/autumn oestrus, which is possibly a single oestrus, considering the relatively low number of adult sows that are either fertilized or show super-fetation in the summer/autumn. If this is true, then matings in late spring should be largely confined to yearling sows, which have their first oestrus later than adult sows. In contrast Wandeler & Graf (1982) found a slight increase in the mean number of both blastocysts and corpora lutea from spring to summer. They took this to indicate that ovulations do occur during delayed implantation, and that at least some are fertilized. More precise field and hormonal data are needed to resolve this question.

The two periods of mating contributed very differently to the overall potential fecundity. For sows ⩾3 years old sampled September–December, 71% and 29% of the total blastocysts were the result of winter/spring and summer/autumn matings, respectively; for yearling sows sampled September–December, of those that became pregnant 70% were fertilized in the winter/spring and 30% in the summer/autumn, with 65% and 35% of the total blastocyst population coming from those two mating periods, respectively. This relative importance of the two mating periods (measured as blastocysts produced) is reflected in the incidence of bite wounding in adult males; minor bite wounding in January–March was 2.3 times as frequent as in August–October, and moderate/extensive bite wounding 3.1 times more frequent.

At first sight it may appear that the reproductive bimodality revealed by this study supports the hypothesis of Roper *et al.* (1986), but in detail there are several crucial inconsistencies. Roper *et al.* (1986) argued that latrine use by badgers was related to the defence of oestrous females by resident males. If that was so, the pattern of latrine use would be expected to reflect the much greater importance of the winter/

Table 7. *The proportion of sows breeding in each annexe sett density class*

	annexe sett density class (mean number of annexe setts per square kilometre per land class)					
	<0.10	0.11–0.15	0.16–0.20	0.21–0.25	0.26–0.30	0.31–0.35
proportion of females ⩾3 years old with signs of having bred	37.8%	—	37.5%	43.5%	56.1%	59.6%
n	45	—	32	23	57	109
proportion of sows with signs of having bred (excluding animals ⩽3 years old)	48.5%	—	54.6%	56.3%	65.0%	65.9%
n	33	—	22	16	43	91

Table 8. *The effects of population density on body condition*

(The figures are means ± s.e. The F-statistic is for a one-way ANOVA; all results $p > 0.05$.)

	main sett density class (mean number of main setts per square kilometre per land class)					annexe sett density class (mean number of annexe setts per square kilometre per land class)						
	< 0.40	0.41–0.45	0.46–0.50	> 0.51		< 0.10	0.11–0.15	0.16–0.20	0.21–0.25	0.26–0.30	0.31–0.35	
health	1.53 ± 0.14	1.39 ± 0.10	1.41 ± 0.09	1.41 ± 0.07	$F = 0.474$	1.53 ± 0.14	—	1.40 ± 0.11	1.40 ± 0.13	1.41 ± 0.09	1.41 ± 0.07	$F = 0.465$
bite wounds	4.50 ± 0.41	4.73 ± 0.31	4.69 ± 0.19	4.88 ± 0.17	$F = 0.698$	4.50 ± 0.41	—	4.72 ± 0.30	4.68 ± 0.24	4.69 ± 0.23	4.88 ± 0.17	$F = 0.677$
adrenal mass	0.51 ± 0.03	0.47 ± 0.02	0.45 ± 0.02	0.47 ± 0.02	$F = 0.481$	0.51 ± 0.03	—	0.46 ± 0.03	0.45 ± 0.02	0.45 ± 0.02	0.47 ± 0.02	$F = 0.473$
omental fat	2.52 ± 0.16	2.61 ± 0.14	2.83 ± 0.13	2.71 ± 0.10	$F = 0.611$	2.52 ± 0.16	—	2.70 ± 0.14	2.64 ± 0.16	2.84 ± 0.14	2.71 ± 0.10	$F = 0.599$
kidney fat	3.27 ± 0.13	3.21 ± 0.17	3.41 ± 0.11	3.30 ± 0.09	$F = 0.598$	3.27 ± 0.13	—	3.23 ± 0.15	3.51 ± 0.16	3.37 ± 0.12	3.30 ± 0.09	$F = 0.593$
whole body mass	9.34 ± 0.42	9.52 ± 0.33	9.76 ± 0.29	9.71 ± 0.21	$F = 1.112$	9.34 ± 0.42	—	9.48 ± 0.28	9.63 ± 0.34	9.76 ± 0.31	9.71 ± 0.21	$F = 1.031$

spring mating period, as does the incidence of bite wounding. Yet Roper *et al.* found (their figure 6) that the spring and autumn peaks were very similar in size. Furthermore, latrine use was greatest in April and October, but the peak in pre-ovulatory follicles in adult sows occurs in January and August (figure 4), with a sharp rise in the incidence of adult sows with blastocysts thereafter (figure 5). Clearly the two peaks in latrine use occur after the main mating periods, not just before or during as would be expected. Thus it seems unlikely that the pattern of latrine use reported by Roper *et al.* (1986) is associated with the defence of oestrous sows.

A consequence of group living in British badgers is the very high loss of reproductive potential. Ahnlund (1980) found that in Sweden 90–95% of adult sows and over 50% of yearling sows develop blastocysts, and that all these animals go on to implant. Although the number of sows with blastocysts is nearly as high in the present study, the proportion that go on to implant is considerably less, and there is a long delay for most sows until they breed successfully (table 4). In fact reproductive failure occurs at three stages in British badgers. Of the total adult sow population, 22% fail to become pregnant, 34% are fertilized but fail to implant their blastocysts, and the remaining 44% of sows go on to full-term pregnancy. However, Cheeseman *et al.* (1987) and Harris & Cresswell (1987) calculated from capture–mark–recapture data that 38% of cubs die pre-emergence from the sett, and they suspected that this was largely due to infanticide. This calculation is closely supported by the post-mortem data presented here, where 35% of sows prematurely ceased to lactate in March and April; thus the post-mortem data strongly suggest that the pre-emergence loss of cubs is due to the death of entire litters rather than individual animals within litters. Neal & Harrison (1958) had also noted a large post-natal loss in badgers, and Wandeler & Graf (1982) found that in Switzerland many adult females examined in spring had fresh placental scars but were not lactating, suggesting a high perinatal mortality due to the loss of entire litters. As approximately 38% of cubs die pre-emergence (i.e. 17% of the total potential productivity), less than 30% of the total potential productivity is achieved.

We have argued that the pre-emergence cub losses are largely due to infanticide, although at present the evidence for infanticide (as opposed to any other cause) is circumstantial. However, several lines of evidence support this contention. The main peak in bite wounding in sows occurs in April, and this appears to reflect an increase in aggressive behaviour on the part of breeding females, perhaps associated with an increase in cub mobility and movements within a sett. It is at this time that the few recorded instances of infanticide in badgers (S. Harris, unpublished observations; Lüps & Roper 1990) have occurred, although infanticide of new born cubs would be much harder to detect. Certainly the spring peak in female aggression coincides with the period of pre-emergence cub mortality, and the distribution of bite wounding within the sow population in April (6

Table 9. *Effects of male group size on group structure and reproductive success; all figures based on adults ⩾3 years old* (Data from the Goucestershire population.)

males per social group	sample size	sex ratio (females per male)	cubs per social group	cubs per adult (sexes combined)	cubs per male	cubs per female
0[a]	74	—	2.36	0.99	—	0.99
1	80	2.34	2.13	0.64	2.13	0.91
2	48	1.56	2.77	0.52	1.33	0.85
3	25	0.99	2.40	0.39	0.77	0.78
4	13	0.96	2.62	0.33	0.65	0.68
5	10	0.84	2.40	0.24	0.44	0.52
6+	11	0.86	2.55	0.21	0.39	0.46

[a] Social groups with cubs but no males ⩾3 years old occurred when the boar had died before the capture operations or as a result of cuckoldry. Also, some of those groups had a yearling male, who could have been capable of siring cubs.

out of 11 breeding sows, 2 out of 3 sows that had stopped lactating prematurely and only 10 out of 40 sows that had not bred) suggests that there is more aggression between the two groups of breeding sows, and that it is the lactating sows that may be responsible for most cases of infanticide. The fact that the presence of annexe setts correlates with an increased reproductive success of younger sows also supports the argument for infanticide, because the younger sows and their cubs are presumably able to avoid the aggression of older, more dominant sows.

Although Roper *et al.* (1986) do not explicitly discuss the role of group living in badgers in relation to their hypothesis, their arguments on territorial behaviour evolve around preventing access to oestrous females by boars in a social system where group living is the norm. In those areas of Britain where territorial behaviour either does not occur or has not been detected, groups seem to be very small, perhaps only pairs (Cresswell *et al.* 1990). Also, when areas are cleared of badgers, recolonization seems to involve the assembling of groups, and only afterwards the defence of territories (Cheeseman *et al.* 1992). Thus territoriality and the presence of larger social groups seem to be closely linked, in Britain at least, and so we have analysed the reproductive gains of group living to badgers. Whilst it is impossible at present to calculate the costs of group living to individual male badgers, the reproductive loss to sows (over 70% of total potential productivity) is very high, and to an individual sow the lifetime loss can be 100%. This loss in reproductive potential is further enhanced by the fact that the breeding sow(s) may not be kin, and there is no evidence that non-breeding sows play any role in rearing the young of dominant sows, or gain experience in cub-rearing before breeding themselves. So what are the factors or benefits that have led to the pattern of social organization seen in British badgers?

These are probably less clear than the arguments put forward either by Kruuk & Parish (1982) and Kruuk (1989) or Roper *et al.* (1986) have implied, and certainly the two ideas are not mutually exclusive. It is particularly difficult to evaluate those two hypotheses when the genetic relationship of badger social groups is unknown. Whilst there is almost certainly a high degree of relatedness within these multi-male/multi-female groups, inter-group movements do occur, usually by reproductively mature animals. How successful they are at breeding within a new social group is at present unknown. However, there is obviously the potential for non-kin breeding within a group. In addition, cuckoldry has been recorded and may be a frequent and successful reproductive strategy (Evans *et al.* 1989), although the reproductive success of different males within the social group is at present unknown. How much of the male bite wounding in the winter/spring is the result of intra-group conflict is unknown. If intra-group conflict is common, it would suggest that there is a dominance hierarchy, in which case it might be presumed that the dominant boars have greater mating success. Yet the few observations on mating in wild badgers suggest that several different boars may mate with a sow during one oestrus (Neal & Harrison 1958; Paget & Middleton 1974), and genetic evidence shows that litters of mixed paternity are not uncommon (Evans *et al.* 1989). Furthermore, so far there is no evidence of mate guarding, even during a sow's most fertile

Table 10. *Effects of male group size on group structure and reproductive success; all figures based on adults ⩾3 years old* (Data from the Bristol population.)

males per social group	sample size	sex ratio (females per male)	cubs per social group	cubs per adult (sexes combined)	cubs per male	cubs per female
0[a]	32	—	1.18	0.84	—	0.84
1	26	2.26	1.50	0.47	1.50	0.68
2	8	1.71	1.50	0.28	0.75	0.44
3+	4	1.00	2.75	0.37	0.73	0.73

[a] Social groups with cubs but no males ⩾3 years old occurred when the boar had died before the capture operations or as a result of cuckoldry. Also, some of those groups had a yearling male, who could have been capable of siring cubs.

Table 11. *Effects of female group size on group structure and reproductive success; all figures based on adults* $\geqslant 3$ *years old* (Data from the Gloucestershire population.)

females per social group	sample size	sex ratio (females per male)	cubs per social group	cubs per adult (sexes combined)	cubs per male	cubs per female
0[a]	31	—	1.03	0.94	0.94	—
1	42	0.81	1.62	1.38	1.31	1.62
2	57	1.52	1.63	2.03	1.24	0.82
3	44	1.38	2.20	2.35	1.01	0.74
4	41	2.60	3.12	1.77	2.03	0.78
5	25	2.40	3.52	2.01	1.69	0.70
6+	26	2.39	4.69	2.22	1.53	0.64

[a] Social groups with cubs but no females $\geqslant 3$ years old occurred when the breeding sow had died before the capture operations.

period. In fact field observations have suggested that matings by visiting boars may not be interrupted by resident boars, and that within groups there is only minor rivalry between boars (Paget & Middleton 1974). Finally, calculating the benefits of territoriality and group living is further complicated by the lack of data on the social structure and mating strategy of badgers living in low densities; they may be pair-bonded, or opportunistic. The latter is feasible because there appears to be little paternal investment in rearing the cubs, or provisioning of the sow.

Bearing all these points in mind, there is no evidence to support the idea that territorial defence is to enable boars to restrict access to oestrous females, nor that there is any net reproductive gain for either males or females from living in larger social groups. Although this cannot yet be calculated for individual males, trends can be assessed at the population level. This shows that for increasing numbers of males per social group, there is a net loss in mean reproductive success per male and per female (tables 9 and 10), and for increasing numbers of females per social group there is no net gain or loss in mean reproductive success per male, but a loss in mean reproductive success per female (tables 11 and 12). This preliminary analysis suggests that the greatest net reproductive gains for badgers would occur if they lived in monogamous pairs or perhaps adopted a solitary social system with opportunistic matings. In Britain these social systems only occur in low-density badger populations and seem to be associated with non-territorial behaviour.

The results from this study cannot be used to test the food-based hypothesis of Kruuk directly. However, there is some evidence that food can be a limited resource for badgers. Kruuk & Parish (1983) showed that food availability causes regional differences in body mass in badgers, and Kruuk & Parish (1985) showed that agricultural changes, causing variations in food availability and quality, were reflected in changes in body mass. Also, when 11 social groups were removed from the Gloucestershire site, in the following years adult mortality in the recolonizing animals was lower, masses were higher than normal and mass gain in cubs was significantly increased. This advantage declined as the badgers regained former densities (Cheeseman *et al.* 1992). Thus the evidence to date questions the reproduction-based hypothesis of Roper and favours the food-based hypothesis of Kruuk as an explanation for territoriality and the social organization of badgers.

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Table 12. *Effects of female group size on group structure and reproductive success; all figures based on adults* $\geqslant 3$ *years old* (Data from the Bristol population.)

females per social group	sample size	sex ratio (females per male)	cubs per social group	cubs per adult (sexes combined)	cubs per male	cubs per female
0	11	—	0.00	0.00	0.00	0.00
1	31	1.11	1.35	0.71	1.50	1.35
2	16	2.46	1.31	0.47	1.62	0.66
3+	18	3.00	2.33	0.33	1.33	0.44

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