

## OFFSPRING SEX RATIO VARIATION IN THE EUROPEAN BADGER, *MELES MELES*

HANNAH L. DUGDALE, DAVID W. MACDONALD,<sup>1</sup> AND CHRIS NEWMAN

Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, UK

**Abstract.** The sex ratio of post-emergence offspring of the European badger *Meles meles* in Wytham Woods, Oxfordshire, UK did not differ significantly from 50% between 1987 and 2001. Insofar as male offspring are more costly to rear successfully, mothers optimized cub productivity with regard to the level of resources that they could invest. When females had a relatively high index of body condition, they implanted early; when implantation was early, the cub sex ratio was male biased. Additionally, years with a male-biased cub sex ratio coincided with a significantly larger cub cohort. These results do not support the local resource competition hypothesis, which proposes that in years when female body condition is poor, females should lower competition for local resources by producing the dispersing sex, i.e., males. The potential mechanisms by which offspring sex ratios may be skewed are discussed. Overall, it appears that bias in the cub sex ratio may result from a combination of adaptive parental strategies, differential infanticide by individuals other than the mother, and differential fetal mortality between the sexes.

**Key words:** body condition; delayed implantation; European badger; local resource competition; *Meles meles*; offspring sex ratio; parental investment; sex differences in fitness; sex differences in mortality; Wytham Woods.

### INTRODUCTION

In polygynous animals, such as the European badger (*Meles meles*), determinants of fitness vary between the sexes (Clutton-Brock 1991). If traits affected by parental investment influence the fitness of one sex more than the other, theory suggests that parental investment may vary toward the sex expected to produce the most grandchildren per unit investment. Differential investment in the sexes has two components: the sex ratio and the amount invested in each sex. Parental investment in badgers has so far eluded measurement, as cubs remain below ground for their first eight weeks postpartum (Neal and Cheeseman 1996), during which time no method has yet been devised either to count or sex them in the wild. In addition, suckling occurs underground and maternity can rarely be assigned without molecular evidence (Domingo-Roura et al. 2003).

Despite these difficulties, differential investment in the sexes can be observed through the sex ratio. Trivers and Willard (1973) proposed that the optimal reproductive strategy for a mother is to produce offspring of the sex that can most benefit from the level of resources that she can provide. They hypothesized that for species with significant sexual dimorphism biased toward males, such that the costs of producing sons exceed those of producing daughters, only qualitatively superior mothers can afford to rear sons, whereas inferior mothers should produce daughters.

Manuscript received 19 November 2001; revised 16 May 2002; accepted 4 July 2002. Corresponding Editor: J. M. Fryxell.

<sup>1</sup> Author to whom correspondence should be addressed. E-mail: david.macdonald@zoology.ox.ac.uk

The hypothesis of Trivers and Willard (1973) embodies two assumptions, the first being that one sex is more costly to produce. In polygynous, sexually dimorphic species, sexual selection should be stronger in males than females (Kruuk et al. 1999). At birth, male badger cubs are heavier than females (Gucwinska and Gucwinska 1968); adult males are more heavily built and have broader heads than adult females (Neal and Cheeseman 1996). In Wytham Woods, Oxfordshire, UK, adult males are 3% longer than adult females, and this difference is achieved by six months of age (Newman et al. 2001). When body length is removed as a covariate, zygomatic arch width is sexually dimorphic (Johnson and Macdonald 2001). Longer adult males produce more subcaudal secretion than shorter males and are more likely to have descended testicles (Woodroffe et al. 1993, Buesching et al. 2002). The second assumption of the Trivers and Willard (1973) hypothesis is that one sex is more strongly influenced by conditions at the end of parental investment than the other, with the consequences of this influence persisting into adulthood. That this applies to badgers is supported by the evidence that, despite mating by multiple males (Johnson 2001; D. W. Macdonald, D. P. Johnson, P. D. Stewart, and S. J. Stafford, *unpublished manuscript*), most cubs are fathered by a minority of males (Evans et al. 1989, Domingo-Roura et al. 2003), whereas up to four females may breed successfully in a group (Cheeseman et al. 1987).

Alternatively, the local resource competition hypothesis (Clarke 1978, Silk 1983) predicts that mothers in poor condition should produce offspring of the sex

that is most likely to disperse from the natal area to reduce competition for resources in that locality. Generally, although juvenile dispersal is rare, male badgers are predominantly the dispersing sex (Cheeseman et al. 1988). Therefore, the local resource competition hypothesis predicts that in years when female badgers are in poor body condition, they should produce the dispersing sex: males. This prediction is opposite to that of Trivers and Willard (1973).

This paper aims to ascertain the factors that predict the annual cub sex ratio of the Wytham badger population between 1987 and 2001, and to determine whether local resource competition (Clarke 1978) or the hypothesis of Trivers and Willard (1973) better explains variation in the cub sex ratio. Sex allocation in polytocous species is more complex than that in monotocous species (Williams 1979, Gosling 1986a). In Europe, badger litter size varies between one and five cubs. The average fetal litter size is 2.7, whereas the average litter size when the cubs are first seen above ground at 8–10 wk is 2.4 cubs (Neal and Cheeseman 1996). In Wytham Woods, mean fetal litter size is  $1.8 \pm 1.0$  (Woodroffe and Macdonald 1995b) and litter size when cubs are first seen above ground is  $1.62 \pm 0.28$  (Macdonald and Newman 2002). Factors that affect the offspring sex ratio in polytocous species include: maternal parity (African wild dogs, *Lycaon pictus*; Creel et al. 1998), maternal age and condition (coypu, *Myocastor coypus*; Gosling 1986b), and stress (golden hamsters, *Mesocricetus auratus*; Pratt et al. 1989).

A measure of maternal body condition may predict the cub sex ratio if investment affects one sex more than the other and if females are able to manipulate the sex ratio of their offspring. Seasonal fluctuations in food availability affect body mass throughout the year, with badgers being lightest in the summer and heaviest in the winter. Breeding females are lighter in spring than are nonbreeders (Page et al. 1994); however, this mass is regained by the autumn and females that breed in one year are no less likely to breed in the next (Woodroffe and Macdonald 1995a). Seasonal fluctuations in body mass are probably caused by fluctuations in the amount of fat stored subcutaneously, intestinally, and around the kidneys (Kruuk and Parish 1983). This may be an adaptation to low food supply in the winter (Woodroffe 1992), when females undertake gestation, relying greatly on stored nutrients. Females that are relatively heavy in the autumn are likely to raise cubs successfully in the following breeding season (Cheeseman et al. 1987).

British badgers can mate during every month of the year (Christian 1995). Mating is polyandrous and some females may mate with five males within a few days (Johnson 2001; D. W. Macdonald, D. D. P. Johnson, P. D. Stewart, and S. J. Stafford, *unpublished manuscript*). There are two peaks in mating activity: one in early spring, from January to May, with a second peak from July to September. These coincide with the fe-

male's estrous cycle (Cresswell et al. 1992). Gestation lasts 4 d pre-implantation and 56 d thereafter. The prolonged period between conception and gestation is due to delayed implantation; blastocysts remain free in the uterine horns, growing very slowly until they are implanted around the winter solstice (Ahnlund 1980). Implantation is triggered by photoperiod and the process can be advanced by up to 6 mo through exposure to long nights (Canivenc et al. 1985). Individuals adapt their implantation date to their local environmental and habitat conditions, with adult females in good body condition implanting earlier than those in poor condition (Woodroffe 1995). The timing of implantation may therefore have some predictive influence on the annual cub sex ratio.

#### METHODS

The data for this study come from long-term work conducted in Wytham Woods, Oxfordshire, UK (01°18' W, 51°46' N) that cover a 4.25 km<sup>2</sup> area. Kruuk (1978) and Hofer (1988) give detailed descriptions of this area and changes that have occurred over time. The population demography is summarized by Macdonald and Newman (2002) and Macdonald et al. (2002b).

From 1987 onward, capture–mark–recapture studies of badgers have occurred at least four times a year; details can be found in Macdonald and Newman (2002). Methods over the long-term study are as follows. Adult badgers were anaesthetised by an intramuscular injection of ~0.2 mL Ketamine hydrochloride (Vetlar, Pharmacia, and Upjohn, Crawley, UK). Cubs judged to weigh  $\leq 2$  kg were considered too small for anaesthesia and were released from traps.

On initial capture, badgers were marked with a tattoo, using Indian ink, on their left inner inguinal region (Cheeseman and Harris 1982). Recaptures were identified by this tattoo. Badgers were classified as cub or adult; they were then sexed and weighed to the nearest 100 g using a handheld spring balance. Because cubs are born under ground in inaccessible burrows, the first measure of cub body mass was at the first trapping of cubs at 16 wk. Head–body length from the tip of the nose to the base of the sacrum was measured on a meter rule, to the nearest 5 mm, with the badger lying flat and ventral side up.

Body condition can be graded using a subcutaneous haunch fat scale, but this has a subjective element. An index of body condition was therefore estimated using the following equation, originally developed for use on otters (Kruuk et al. 1987):

$$\log W = \log k + n \log L$$

where  $W$  is body mass (in kilograms),  $L$  is length (in millimeters), and  $k$  and  $n$  are constants. Regressing log-transformed body mass and log-transformed body length of every adult female trapped between 1995 and 2000 produced the constants  $k = 1.6649 \times 10^{-7}$  and  $n = 2.7044$ , which provided an estimate of expected

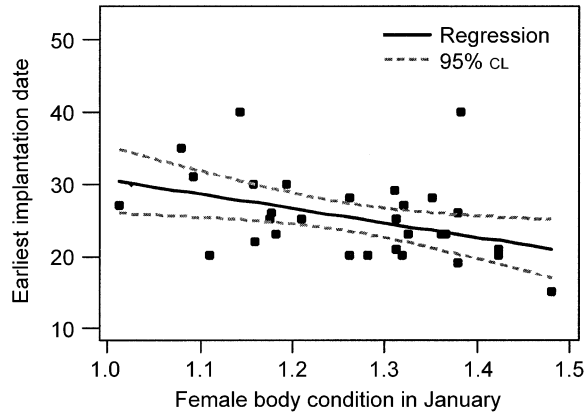


FIG. 1. The body condition index of each pregnant female European badger in January as a predictor of the earliest implantation date (number of days after 1 December) of that female in the years 1993–1995, 1997–1999, and 2001 ( $Y = 50.4790 - 19.9126X$ ,  $r^2 = 17.6\%$ ). In the regression analysis, one entry, selected at random, was deleted for the four individuals that underwent ultrasound twice over the years, but all data are displayed in the fitted-line plot.

mass. Body condition index was calculated using observed mass divided by expected mass (Woodroffe 1995). Pregnancy was diagnosed by ultrasound scanning of females in January using an external 5.0 MHz sector probe (Kontron, Watford, UK). The crown–rump lengths of fetuses were then used to estimate the implantation date using the formula obtained by Dunmartin et al. (1989):

$$a = 3.21 \pm 0.50l - 0.004l^2 \pm 0.00002l^3$$

where  $a$  is age (in days) and  $l$  is length (in millimeters). Annual ultrasound scanning in midwinter was introduced in 1993, but could not be undertaken during 1996 and 2000. The retrospective mean number of badgers alive in any one year was also calculated (Krebs 1966).

Minitab was used for all statistical analyses. When regressions were performed, histograms of the residuals were checked for normality and scatter plots of the residuals vs. the fitted values were checked for similarity of variance.

## RESULTS

Overall, the cub sex ratio of the Wytham badger population did not differ significantly from 50:50 in the period 1987–2001, as shown by a one sample  $t$  test, with the null hypothesis that the ratio mean did not differ from parity ( $50.95 \pm 7.80$ , mean  $\pm$  1 SD;  $t_{15} = 0.47$ ,  $P = 0.644$ ).

“Fatter” females that had a greater index of body condition in January implanted significantly earlier than females with a lower index ( $F_{1,26} = 4.95$ ,  $P = 0.035$ ; Fig. 1). Implantation date was a significant predictor of the cub sex ratio ( $F_{1,5} = 7.68$ ,  $P = 0.039$ ; Fig. 2); when implantation was early in December, the cub sex ratio in the following spring was male biased.

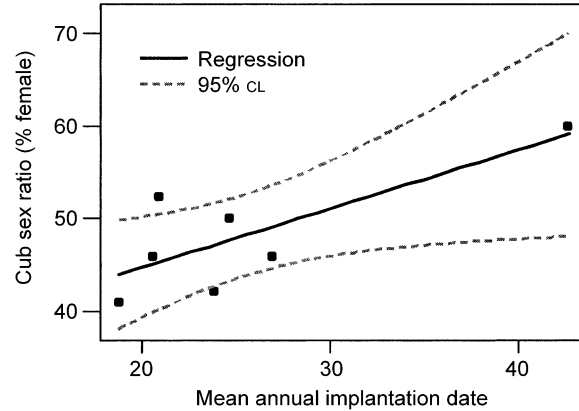


FIG. 2. The mean annual implantation date (number of days after 1 December) of all pregnant female badgers as revealed by ultrascanning, as a predictor of the badger cub sex ratio in the years 1993–1995, 1997–1999, and 2001 ( $Y = 32.0464 + 0.633233X$ ,  $r^2 = 60.6\%$ ).

However, the mean index of female body condition was not significantly related to the annual cub sex ratio (November,  $F_{1,5} = 1.52$ ,  $P = 0.273$ ; January,  $F_{1,7} = 0.42$ ,  $P = 0.537$ ). Neither was it significant when a GLM (Generalized Linear Model) was employed to adjust for the effect of population size, using a minimum number alive estimate for the year in which the body condition index was calculated (November,  $F_{1,4} = 1.49$ ,  $P = 0.289$ ; January,  $F_{1,6} = 0.35$ ,  $P = 0.575$ ).

Cub cohort size between 1987 and 2001 was a significant predictor of the badger cub sex ratio ( $F_{1,13} = 5.63$ ,  $P = 0.034$ ; Fig. 3); in years when the cub cohort size was large, the cub sex ratio was male biased. This relationship still touched significance ( $F_{1,9} = 5.07$ ,  $P = 0.051$ ) when a GLM was used to correct for any effect of cub body condition at first capture on sex ratio. The mean cub body condition index at week 16 was not significantly related to cub cohort size ( $F_{1,10} = 0.12$ ,  $P = 0.736$ ).

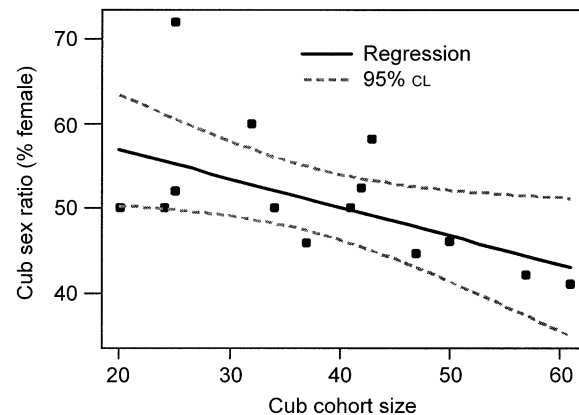


FIG. 3. The annual badger cub cohort size as a predictor of the corresponding cub sex ratio between 1987 and 2001 ( $Y = 63.5617 - 0.336629X$ ,  $r^2 = 30.2\%$ ).

There was no significant relationship between the mean index of female body condition in either November ( $F_{1,4} = 1.39$ ,  $P = 0.304$ ) or January ( $F_{1,6} = 1.68$ ,  $P = 0.242$ ) and the annual cub cohort size when a GLM was used to correct for the effect of population size. Female body condition index in January was not significantly related to the number of implanted embryos in a female in January ( $F_{1,26} = 0.03$ ,  $P = 0.874$ ).

#### DISCUSSION

There was no overall post-emergence bias in cub sex ratio in the Wytham badger population; however, deviations from the 50:50 cub sex ratio were seen in certain years. In particular, females in superior condition implanted earlier (as reported by Woodroffe 1995); when the mean implantation date was early, a male-biased cub sex ratio was produced, as predicted by Trivers and Willard (1973). However, there was no significant relationship between the mean index of female body condition in either November or January and the resulting cub sex ratio. This analysis is at the population level, and might disguise relationships that apply only in some social groups due to local variability in environmental conditions. Indeed, analysis at the population level may be confounded insofar as there is group-to-group variation, during any one year, in the local impact of the increasing badger population density that, between 1987 and 1996, was associated with an overall decrease in body mass and female condition in the study area (Macdonald et al. 2002b). When the retrospective mean number alive was considered in the relationship between female body condition and cub cohort size, the relationship was not improved.

The local resource competition hypothesis predicts that in years when females are in relatively poor condition, the cub sex ratio should be biased toward the dispersing sex to reduce local resource competition (Clarke 1978, Silk 1983). Generally, in mammals, it is the males that disperse the farthest (Greenwood 1980). Emigration of adult badgers, although juvenile dispersal is rare (Evans et al. 1989), is generally confined to males (Cheeseman et al. 1988). Hence, years in which female body condition is relatively poor would, under the local resource competition hypothesis, be expected to result in a male-biased cub sex ratio. On the contrary, to the extent that there was any relationship, it was in the opposite direction, such that females tended to produce males when they were in relatively good condition, as predicted by Trivers and Willard (1973).

Years with large cub cohorts were significantly associated with a male-biased cub sex ratio. If one argues that when females were in relatively good condition they implanted early, and when implantation was early, the cub sex ratio was also male biased, one must also consider the trade-off between the number of independent offspring produced per reproductive attempt and their size (Smith and Fretwell 1974). An inverse re-

lationship between litter size and cub size would be expected from this trade-off; hence, years with large litter sizes might be expected, all else being equal, to result in smaller offspring and a female-biased cub sex ratio. This relationship provides an insight into the relative maternal investment in the sexes. However, the relationship between the index of cub body condition at 16 wk and the cub cohort size was not significant. Interpretation of this result is complicated because conditions during the first 16 wk of a cub's life may be independent of those during the period when the cub sex ratio was determined; furthermore, it may be confounded by other population processes. For example, coccidiosis infection, which is associated with impaired cub growth, varies interannually in prevalence (Newman et al. 2001), and cub growth may be affected by overall, as well as local, changes in population density (Macdonald et al. 2002b).

There was no significant relationship between female body condition and cub cohort size at the population level. Analysis of female body condition at the population level may be misleading because the effect of local environmental conditions and social structure may mask underlying trends. Ideally, this relationship should be studied at the individual level; this is becoming feasible as the difficulties of using molecular techniques to assign maternity in badgers are overcome (Domingo-Roura et al. 2003). Individual body condition early in gestation and the number of implanted embryos were not significantly related. However, post-natal mortality does occur, and the number of embryos detected early in gestation may not be representative of litter size.

The appropriateness of the Trivers and Willard (1973) hypothesis to the social system of Wytham's population of European badgers is uncertain. On the one hand, genetic evidence (da Silva 1989, Evans et al. 1989) suggests that, although more than one male fathers cubs in a group, only a minority of males do so. Dispersal patterns and associated physical attributes led Woodroffe et al. (1993) to infer that a single, immigrant male might dominate matings in each group. On the other hand, evidence of linear dominance relations within badger groups has proven elusive (Macdonald et al. 2002a) and females may mate with up to five males within one estrus (Johnson 2001; D. W. Macdonald, D. D. P. Johnson, P. D. Stewart, and S. J. Stafford, *unpublished manuscript*).

Williams (1979) elaborated on the model of Trivers and Willard (1973) by predicating that the pattern of offspring production from mothers in poor condition to those in superior condition, where sons are more expensive to produce than daughters, is: one daughter, then one son, then two daughters, then one daughter and one son, then two sons, and so on. Thus, female-biased litters could result from mothers producing smaller than average litters (Gosling 1986a). Additionally, in order to maximize their lifetime reproduc-

tive success, females may not invest up to their maximum potential in one litter (Charnov and Krebs 1974). The cub sex ratios discussed in this paper are at the population level because, in the absence of genetic evidence, we are unable to assign cubs to their mothers. Notwithstanding inevitable small-scale variation in the sociological and environmental circumstances of different groups, environmental conditions are relatively uniform over the comparatively small 425-ha study site, so we would expect individual cub sex ratio variation to follow the population trend.

In animals in which sex is chromosomally determined, the mechanism of offspring sex ratio control is poorly understood. Multiple paternity occurs within badger litters (Evans et al. 1989), which may enable females to vary their offspring sex ratio at conception. The winter–spring matings contribute 71% of the blastocysts seen on postmortem examination of adult females, with summer–autumn matings accounting for the rest (Cresswell et al. 1992). It is thus possible that females can manipulate the sex ratio of their litters at matings later in the year through reabsorption of blastocysts or embryos of one sex, as seen in the coypu (Gosling 1986b). This would require the female's body to recognize how many blastocysts or embryos she was carrying, along with their sex. Finally, females may manipulate their offspring sex ratio through differential infanticide; however, it may be that rival mothers, non-breeding females, or males in the group carry out this infanticide, a point made by Woodroffe (1992). Siblicide may also play a role. However, the literature, albeit it not drawn from our study area, indicates that 35–42% of the females that have implanted prematurely cease lactating (Cresswell et al. 1992, Page et al. 1994), suggesting that loss of whole litters, rather than individuals, is the greatest component of postnatal loss.

Offspring sex bias may result from differential survival of males and females as fetuses (McMillan 1979) or as juveniles (Clutton-Brock et al. 1985, McClure 1981). We ascertained offspring sex ratio post-emergence, so both mortality regimes may affect the observed cub sex ratios. Only 34–60% of females with blastocysts implant and, of these, 0–36% suffer fetal mortality (Cresswell et al. 1992, Page et al. 1994, respectively). Thus, fetal mortality does occur, but whether or not this is sex biased is unknown. Between 1989 and 1996, the overall juvenile mortality between the sexes in Wytham did not differ (Macdonald and Newman 2002). Thus, there is potential for manipulation of the offspring sex ratio, but differential survival of neonates may play a role, too. The mechanism by which the offspring sex ratio is skewed is unclear and it is likely to be a result of several mechanisms that are all affected by environmental conditions.

#### ACKNOWLEDGMENTS

We are extremely grateful to Paul Johnson for helping with the statistics and for his comments on the manuscript. The manuscript greatly benefited from comments by Morris Gos-

ling and an anonymous referee. We would like to thank everyone who helped with the collection of the Wytham badger data over 15 yr, in particular: Sandra Baker, Christina Buesching, Jack da Silva, Stephen Ellwood, Bart Harmsen, Dom Johnson, Xavier Domingo-Roura, Dave Slater, Paul Stewart, Sharon Quinn, Lilian Villalba, Rosie Woodroffe, and Beatriz Zapata. Much of this core study was generously supported by the Peoples Trust for Endangered Species. Work was carried out under English Nature Licences, currently 20001537 and Home Office Licence PPL 30/1216.

#### LITERATURE CITED

- Ahnlund, H. 1980. Sexual maturity and breeding season of the badger, *Meles meles* in Sweden. *Journal of Zoology, London* **190**:77–95.
- Buesching, C. D., C. Newman, and D. W. Macdonald. 2002. Variations in colour and volume of the subcaudal gland secretion of badgers (*Meles meles*) in relation to sex, season and individual-specific parameters. *Zeitschrift für Säugetierkunde* **67**:1–10.
- Canivenc, R., M. Bonnin, and M. C. Audy. 1985. Mechanism of photoperiodic control of delayed implantation in the European badger *Meles meles* L. *Pathologie Biologie* **33**:976–976.
- Charnov, E. L., and J. R. Krebs. 1974. On clutch-size and fitness. *Ibis* **116**:217–219.
- Cheeseman, C. L., W. J. Cresswell, S. Harris, and P. J. Mal-linson. 1988. Comparison of dispersal and other measurements in two badger (*Meles meles*) populations. *Mammal Review* **18**:51–59.
- Cheeseman, C. L., and S. Harris. 1982. Methods of marking badgers (*Meles meles*). *Journal of Zoology, London* **197**:289–292.
- Cheeseman, C. L., J. W. Wilesmith, J. Ryan, and P. J. Mal-linson. 1987. Badger population dynamics in a high-density area. *Symposium of the Zoological Society of London* **58**:279–284.
- Christian, S. F. 1995. Observations of extra-group mating and mate-defence behaviour in badgers, *Meles meles*. *Journal of Zoology, London* **237**:668–670.
- Clarke, A. B. 1978. Sex ratio and local resource competition in a prosimian primate. *Science* **201**:163–165.
- Clutton-Brock, T. H. 1991. *Reproductive success*. University of Chicago Press, Chicago, Illinois, USA.
- Clutton-Brock, T. H., S. D. Albon, and F. D. Guinness. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* **313**:131–133.
- Creel, S., N. M. Creel, and S. L. Monfort. 1998. Birth order, estrogens and sex-ratio adaptation in African wild dogs (*Lycaon pictus*). *Animal Reproduction Science* **53**:315–320.
- Cresswell, W. J., S. Harris, C. L. Cheeseman, and P. J. Mal-linson. 1992. To breed or not to breed—an analysis of the social and density-dependent constraints on the fecundity of female badgers (*Meles meles*). *Philosophical Transactions of the Royal Society of London B* **338**:393–407.
- da Silva, J. 1989. *Ecological aspects of Eurasian badger social structure*. Dissertation. University of Oxford, Oxford, UK.
- Domingo-Roura, X., D. W. Macdonald, M. S. Roy, J. Marmi, J. Terradas, R. Woodroffe, T. Burke, R. K. Wayne. 2003. Confirmation of low genetic diversity and multiple breeding females in a social group of Eurasian badgers from microsatellite and field data. *Molecular Ecology*.
- Dunmartin, B., C. Ribes, J. Souloumiac, G. Charron, and R. Canivenc. 1989. Experimental study of foetal growth in the European badger *Meles meles* L. *Mammalia* **53**:279–285.
- Evans, P. G. H., D. W. Macdonald, and C. L. Cheeseman. 1989. Social structure of the Eurasian badger (*Meles me-*

- les): genetic evidence. *Journal of Zoology, London* **218**: 587–595.
- Gosling, L. M. 1986a. Biased sex ratios in stressed animals. *American Naturalist* **127**:893–896.
- Gosling, L. M. 1986b. Selective abortion of entire litters in the coypru: adaptive control of offspring production in relation to quality and sex. *American Naturalist* **127**:772–795.
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* **28**:1140–1142.
- Gucwinska, H., and A. Gucwinska. 1968. A note on the development and growth of European badgers *Meles meles* born at Wroclaw Zoo. *International Zoo Yearbook* **8**:133.
- Hofer, H. 1988. Variation in resource presence utilisation and reproductive success within a population of European badgers. *Mammalian Review* **18**:25–36.
- Johnson, D. D. P. 2001. Models of coexistence, conflict and cooperation. Dissertation University of Oxford, Oxford, UK.
- Johnson, D. D. P., and D. W. Macdonald. 2001. Why are group-living badgers (*Meles meles*) sexually dimorphic? *Journal of Zoology, London* **255**:199–204.
- Krebs, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. *Ecological Monographs* **36**:239–273.
- Kruuk, H. 1978. Spatial organisation and territorial behaviour of the European Badger *Meles meles*. *Journal of Zoology, London* **184**:1–19.
- Kruuk, H., J. W. H. Conroy, and A. Moorhouse. 1987. Seasonal reproduction, mortality and food of otters (*Lutra lutra L.*) in Shetland. Symposium of the Zoological Society, London **58**:263–278.
- Kruuk, H., and T. Parish. 1983. Seasonal and local differences in the weight of European badgers (*Meles meles L.*) in relation to food supply. *Zeitschrift für Säugetierkunde* **48**: 45–50.
- Kruuk, L. E. B., T. H. Clutton-Brock, K. E. Rose, and F. E. Guinness. 1999. Early determinants of lifetime reproductive success differ between the sexes in red deer. *Nature* **266**:1655–1661.
- Macdonald, D. W., and C. Newman. 2002. Population dynamics of badgers (*Meles meles*) in Oxfordshire; numbers, density and cohort life histories, and a possible role of climate change in population growth. *Journal of Zoology, London* **256**:121–138.
- Macdonald, D. W., C. Newman, P. D. Stewart, and X. Domingo-Roura. 2002b. Density-dependent regulation of body weight and condition in badgers (*Meles meles*) from Wytham Woods, Oxfordshire. *Ecology* **83**:2056–2061.
- Macdonald, D. W., P. D. Stewart, and C. D. Buesching. 2002a. No evidence of social hierarchy amongst feeding badgers, *Meles meles*. *Ethology* **108**:613–628.
- McClure, P. A. 1981. Sex-biased litter reduction in food-restricted wood rats (*Neotoma floridana*). *Science* **211**: 1058–1060.
- McMillan, M. M. 1979. Differential mortality by sex in fetal and neonatal deaths. *Science* **204**:89–91.
- Neal, E., and C. Cheeseman. 1996. Badgers. T. & A. D. Poyser Ltd. London, UK.
- Newman, C., D. W. Macdonald, and M. A. Anwar. 2001. Coccidiosis in the European badger *Meles meles* in Wytham Woods: infection and consequences for growth and survival. *Parasitology* **123**:133–142.
- Page, R. J. C., J. Ross, and S. D. Langton. 1994. Seasonality of reproduction in the European badger *Meles meles* in south-west England. *Journal of Zoology, London* **233**:69–91.
- Pratt, N. C., U. W. Huck, and R. D. Lisk. 1989. Do pregnant hamsters react to stress by producing fewer males? *Animal Behaviour* **37**:155–157.
- Silk, J. B. 1983. Local resource competition and facultative adjustment of the sex-ratios in relation to competitive abilities. *American Naturalist* **121**:56–66.
- Smith, C. C., and S. D. Fretwell. 1974. The optimal balance between size and number of offspring. *American Naturalist* **108**:499–506.
- Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science* **179**:90–92.
- Williams, G. C. 1979. The question of adaptive variation in sex ratio in outcrossed vertebrates. *Proceedings of the Royal Society of London, B* **205**:567–580.
- Woodroffe, R. 1992. Factors affecting reproductive success in the European badger *Meles meles*. Dissertation. University of Oxford, Oxford, UK.
- Woodroffe, R. 1995. Body condition affects implantation date in the European badger, *Meles meles*. *Journal of Zoology, London* **236**:183–188.
- Woodroffe, R., and D. W. Macdonald. 1995a. Costs of breeding status in the European badger *Meles meles*. *Journal of Zoology, London* **235**:237–245.
- Woodroffe, R., and D. W. Macdonald. 1995b. Female–female competition in European badgers *Meles meles*—effects on breeding success. *Journal of Animal Ecology* **64**:12–20.
- Woodroffe, R., D. W. Macdonald, and J. da Silva. 1993. Dispersal and philopatry in the European badger, *Meles meles*. *Journal of Zoology* **237**:227–239.