© 2005 Universities Federation for Animal Welfare The Old School, Brewhouse Hill, Wheathampstead, Hertfordshire AL4 8AN, UK

Welfare of badgers (Meles meles) subjected to culling: development and evaluation of a closed season

R Woodroffe^{*†}, FJ Bourne[†], CL Cheeseman[‡], DR Cox^{†§}, CA Donnelly^{†#}, G Gettinby^{†¶}, JP McInerney^{†¥} and WI Morrison^{†¤}

* Department of Wildlife, Fish and Conservation Biology, University of California, One Shields Avenue, Davis, CA 95616, USA

[†] Independent Scientific Group on Cattle TB, c/o Department for Environment, Food and Rural Affairs, IA Page Street, London SWIP 4PQ, UK

[‡] Central Science Laboratory, Sand Hutton, York YO41 1LZ, UK

[§] Nuffield College, New Road, Oxford OX1 INF, UK

[#] Department of Infectious Disease Epidemiology, Faculty of Medicine, Imperial College London, Norfolk Place, St Mary's Campus, London W2 IPG, UK

¹ Department of Statistics and Modelling Science, University of Strathclyde, George Street, Glasgow G1 IXH, UK

* Agricultural Economics Unit, University of Exeter, Lafrowda House, St German's Road, Exeter EX4 6TL, UK

^a Centre for Tropical Veterinary Medicine, Royal (Dick) School of Veterinary Studies, University of Edinburgh, Easter Bush, Roslin, Midlothian EH25 9RG, UK

* Contact for correspondence and requests for reprints: rwoodroffe@ucdavis.edu

Abstract

For the past 25 years, European badgers (Meles meles) have been subject to culling in Britain in attempts to limit the spread of tuberculosis (TB) to cattle. As part of a far-reaching evaluation of the effectiveness and acceptability of badger culling as a TB control measure, this paper assesses one aspect of the welfare of badger populations subjected to culling: the killing of breeding females, which risks leaving their unweaned cubs to starve in the den. To avoid this possibility, a three-month closed season was adopted, running from 1st February to 30th April, based on the best available estimates of the timing of birth and weaning in British badgers. During May 1999–2003, when a total of 4705 adult badgers were culled, field teams failed to capture 12 unweaned litters when their mothers were despatched. In 31 other cases, lactating females were culled but litters of almost-weaned cubs missed by culling teams — estimated at approximately nine per year on average — was dramatically lower than that projected by a badger welfare lobby group. Our data suggest that the closed season is effective in reducing the suffering of unweaned cubs in badger populations subject to culling, and we recommend that this measure be maintained should badger culling form a component of any future TB control policy.

Keywords: animal welfare, bovine tuberculosis, closed season, delayed implantation, embryonic diapause, European badger

Introduction

European badgers (Meles meles) have been subject to culling in Britain for over 25 years, as part of ongoing efforts to reduce transmission of tuberculosis (TB; Mycobacterium bovis) to cattle (Krebs et al 1997). Badgers' role in maintaining TB in cattle, and the effectiveness of badger culling as a TB control measure, are currently being assessed in an extensive field trial (The Randomised Badger Culling Trial: Bourne et al 1998, 2000a,b; Woodroffe et al 2003). The trial is formally evaluating not only the technical effectiveness of badger culling in reducing the incidence of cattle TB, but also its cost effectiveness (to the farming economy and to government) and its acceptability in the widest sense (Bourne et al 2000b; Woodroffe et al 2003). If badger culling is to be acceptable, both as a candidate TB control policy and as an experimental treatment, badger welfare must be taken into account in devising culling strategies.

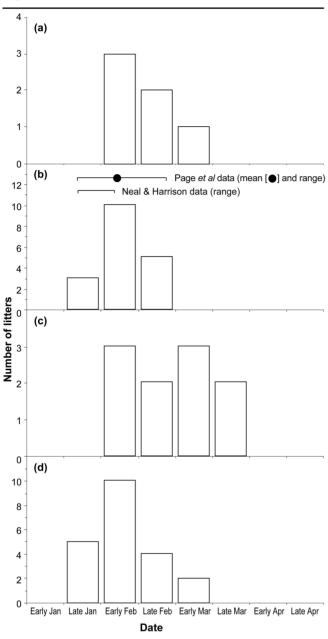
Since 1982, badgers to be culled have been captured in cage traps and then despatched by gunshot (Krebs et al 1997). An independent audit of this procedure indicated that death was instantaneous in "almost all, if not all, cases", and the despatch was considered "humane" (Kirkwood 2000; Ewbank 2003). However, this does not preclude suffering of badger cubs dependent upon those that are culled. Badger cubs are born underground and do not emerge from the den (sett) until they are around 6-8 weeks old. While there is evidence to suggest that non-breeding females may sometimes be involved in juvenile care (Woodroffe 1993), it is almost certain that cubs below ground are completely dependent upon their mothers for nourishment. Killing a breeding female badger during this period of dependency will therefore leave her cubs to die of starvation or dehydration below ground. This gives cause for concern, since such a death is likely to involve serious suffering. In contrast,

Universities Federation for Animal Welfare



20 Woodroffe et al





Frequency distributions of observed and estimated birth dates of badgers, calculated by four different methods: (a) dates of births observed in captivity (data from Neal & Harrison 1958; Kruuk 1989); (b) dates of births projected forwards on the basis of measurements of foetus size — histogram gives data from Woodroffe (1995), horizontal bars give data from Page *et al* (1994; n = 34) and Neal and Harrison (1958; n = 6); (c) dates of births calculated backwards from records of cubs estimated to be <6 weeks old (data from Neal & Harrison 1958); (d) dates of births calculated backwards from dates of cubs' first emergence above ground (data from Neal & Harrison 1958).

once cubs are weaned and moving regularly outside the den, they are easily captured in cage traps (Tuyttens *et al* 1999) and can be despatched humanely.

Previous badger culling strategies attempted to avoid this eventuality by releasing lactating females at the point of capture (Krebs *et al* 1997). However, there are several

© 2005 Universities Federation for Animal Welfare

disadvantages to this approach. First, it is difficult to distinguish lactating females from other badgers without removing them from the cage trap; despite a policy of releasing lactating females, during 1996-1998, 59 females were recorded as lactating at post mortem, comprising 4.3% of the 1363 adult females culled in the same months (Department for Environment, Food and Rural Affairs [DEFRA], unpublished data). Second, release of lactating females undermines the objective of removing TB-infected badgers from the vicinity of TB outbreaks in cattle. Such releases could be particularly damaging if, as has been suggested, mother-cub transmission is important in maintaining TB infection in badger populations (Smith et al 1997). Third, the partial removal of social groups entailed in releasing lactating females could increase the rate and distances that badgers move, affecting contact rates between badgers and possibly TB transmission (Tuyttens et al 2000).

To avoid the problems inherent in releasing lactating females, we proposed a closed season during which no culling would take place (Bourne et al 1998). Our aim was to reduce the starvation of cubs below ground to a practical minimum; bearing in mind that the strategy adopted had to be workable as a candidate policy. One criticism of former culling policies was that long delays between TB outbreaks in cattle and the culling of badgers might have undermined the potential effectiveness of badger culling as a TB control measure (Krebs et al 1997); this apparent need to act quickly constrained the length of closed season that could be adopted. The closed season was therefore timed to coincide with the period when badger cubs are below ground and totally dependent upon their mothers, ending at a time when cubs themselves could be readily captured and despatched humanely. This measure was severely criticised by the National Federation of Badger Groups (NFBG), which estimated that, despite the closed season, 2300 orphaned badger cubs could be expected to starve to death in the first phase of the field trial (National Federation of Badger Groups 1999). Here, we describe the formulation of the closed season and assess its effectiveness in limiting the suffering imposed by badger culling.

Developing the closed season

Since the closed season aimed to avoid culling females with unweaned cubs still confined to the den, its timing was based upon estimates of birth and weaning dates among British badgers. Badger reproduction is highly seasonal and synchronised; conception may occur at any time between February and October, but implantation is delayed until around the time of the winter solstice (Neal & Harrison 1958). Implantation date is triggered by changes in photoperiod (Canivenc *et al* 1981) and apparently modulated by females' body condition prior to implantation (Woodroffe 1995). We selected data on pregnancy and birth dates of British badgers from the literature, excluding those considered unreliable.

Approximate estimates of birth dates can be derived from pregnancy rates reported by post mortem studies. Such studies have reported post-implantation pregnancies only in the months of January and February, despite large samples of females necropsied in other months (the total number of females examined in March–December was 701 [Neal & Harrison 1958; Page *et al* 1994]). Since gestation lasts 45 days (Dumartin *et al* 1989), this indicates that births outside the months of January–March must be extremely uncommon.

The most precise data on birth dates would come from observations of births in the wild. However, such data are almost impossible to obtain, since births occur deep underground. The only published birth dates therefore come from badgers held in captivity; these data (from Neal & Harrison 1958; Kruuk 1989) indicate births occurring from early February to early March, and are shown in Figure 1a.

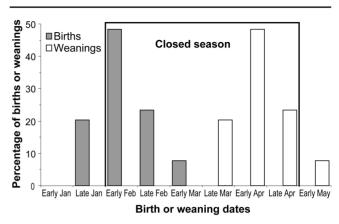
A second source of reasonably reliable data on birth dates is the measurement of foetuses *in utero* in either live or dead wild badgers; their birth dates can be projected quite accurately because foetal growth trajectories have been studied (Dumartin *et al* 1989). Projected birth dates (from Neal & Harrison 1958; Page *et al* 1994; Woodroffe 1995) indicate births occurring from late January to early March, and are shown in Figure 1b. Implantation dates published by Woodroffe (1995) have been converted to birth dates by assuming a gestation period of 45 days (Dumartin *et al* 1989); note that the two other studies report only the earliest and latest projected birth dates.

Less reliable estimates of birth and weaning dates are derived from reports of small cubs around their dates of first emergence from the den. These data (indicating a range of birth dates from late January to late March, and shown in Figures 1c and 1d) are unreliable because growth trajectories and behavioural development have not been studied in known-age cubs. Estimates of birth dates based on cubs' size later in the year and on females' lactation status (eg Neal & Harrison 1958) were not used because cubs' growth rates depend largely upon nutrition (Woodroffe & Macdonald 2000) and because the duration of lactation has not been studied in badgers.

The data presented in Figures 1a and 1b suggest that most births occur in February, with the latest births in March. We used the most reliable data on birth dates - observations in captivity, and projections from measurements made in utero (Figures 1a and 1b) — as the basis for the closed season. To improve the sample size, we attempted to reconstruct the frequency distribution of data presented in Page et al (1994) and Neal and Harrison (1958) (shown in Figure 1b as bars). We allocated births recorded in Neal and Harrison (1958) to half-months with equal probabilities within the range given by the authors. We adopted a similar procedure with data from Page et al (1994), but modified the distribution to generate the mean and range reported in the original paper. The resulting frequency distribution (shown in Figure 2) is therefore somewhat inaccurate, with the proportion of births at the extremes of the distribution likely to be over-estimated. Nevertheless, we adopted this distribution as a conservative working estimate of the true distribution of births.

A closed season for badger culling 21





Frequency distribution of estimated birth and weaning dates, using the most reliable data available. Birth dates are derived from Kruuk (1989), Neal and Harrison (1958), Page *et al* (1994) and Woodroffe (1995). Weaning dates are projected to be two months after birth dates. The nominated closed season, indicated, covers the months of February, March and April.

The birth dates shown in Figure 2 can be used to project an expected distribution of weaning dates, by assuming that weaning occurs at two months of age (this figure is necessarily approximate, since precise weaning dates of knownage cubs are not reported in the literature). This suggests that, on the basis of the available data, almost all cubs should be weaned by mid-May, with all births occurring after mid-January.

Using the data presented in Figure 2, we proposed a closed season covering the months of February, March and April. The available data suggest that as many as 20% of births, and 8% of weanings, could occur outside the closed season (although these may be over-estimates since the 'tails' of the distribution are inaccurate — see earlier). Numbers of lactating females culled outside the closed season were anticipated to be somewhat lower than suggested by these figures, since we expected that few trapping operations would be carried out in January, when capture success is low (Tuyttens *et al* 1999).

To ensure the most effective operation of the closed season, we stipulated that all culling in the months of May and June be carried out continuously, without breaks at weekends (Bourne *et al* 1998). This was to maximise the chances that cubs would be captured as rapidly as possible if their mothers were culled.

Evaluating the closed season

The closed season could fail in two ways. First, cubs might be born before the start of the closed season but, being too young to be captured themselves, would starve if their mothers were killed. Second, late-born cubs might still be living below ground, unavailable for capture, when the closed season ends. Evaluation of the closed season's performance therefore demands consideration of the number of lactating females and young cubs captured both before and after the season.

Methods

We determined the number of cubs and lactating females captured in the course of field-trial culling operations in May (immediately after the end of the closed season) 1999, 2000, 2002 and 2003, and in January (immediately before the closed season) 2000, 2001 and 2003. No data were available from May 2001 or January 2002 because trapping was suspended throughout this period due to the outbreak of foot-and-mouth disease (FMD) in Great Britain.

Badgers were captured in cage traps and despatched by DEFRA staff using standard protocols and operating under Crown Immunity (Bourne *et al* 1998; Kirkwood 2000). In May, cubs were readily distinguished from adults on the basis of their small size (mean weights [\pm SD]: cubs 3.5 ± 1.1 kg; adults 9.1 ± 1.6 kg; $t_{763} = 48.7$; P < 0.0001) and unworn teeth. Cubs were also distinguishable from adults in January (mean weights [\pm SD]: cubs 9.9 ± 1.6 kg; adults 11.2 ± 1.8 kg ; $t_{320} = 3.3$; P = 0.001), but all of the cubs captured were large (the lowest weight was 7.0 kg), indicating that they had been born the previous year and would be independent of their mothers.

Females with dependent cubs were identified at post mortem by their lactation status. Longitudinal studies based on ultrasound scanning have detected no evidence of lactation in females that have not been pregnant, indicating that lactation is a good indicator of maternity (Woodroffe [1992]; in contrast, lactation may occur without pregnancy in other carnivore species, eg Creel et al [1991]). At necropsies carried out from 2000 onwards, veterinarians attempted to express milk from the teats, and also cut into the mammary tissue. We considered females to be actively lactating if milk could be expressed from the teats, or exuded from the cut surfaces of mammary tissue. Females with extended teats were also recorded. However, once females have stopped lactating it is unfortunately not possible to distinguish them with any confidence from those that have lactated in previous years, since females' teats remain extended throughout their lives once they have lactated (Woodroffe 1992). This necropsy protocol was introduced in 2000; prior to that time, the basis on which females were considered to be 'lactating' had not been defined in standard operating procedures. For this reason, some badgers considered to be 'lactating' in 1999 may not have been actively lactating, even if they had extended teats. This would tend to over-estimate the number of females with unweaned cubs. Nevertheless, data from 1999 are presented here for the sake of completeness.

Culling of lactating females leads to cub starvation only if the cubs themselves are not captured and despatched. Cubs captured at the same den as a lactating female were assumed to be the offspring of that female. Where more than one potentially breeding female was caught at the same den, cubs were attributed to the most probable mother (based on lactation status) or divided equally among females that had the same lactation status.

Results

Evidence of lactation before the closed season

Data were available on 212 adult female badgers culled in the course of the field trial during January (18 in 2000, 78 in 2001, and 116 in 2003) in 11 trial areas. None of these females was found to be lactating, although 98 (46%) were pregnant. Thus, 0/212 females (0%; 95% exact binomial confidence limits 0–1.7%) might have had cubs below ground at the time of a January cull.

Evidence of lactation after the closed season

Data on active lactation were available on 735 adult females captured in May (303 in 2000, 161 in 2002, and 271 in 2003), in eight trial areas. Of these, 37 were found to be actively lactating (4 in 2000, 14 in 2002, and 19 in 2003). There was significant variation among years in the proportion of females found to be in active lactation ($\chi^2 = 15.47$; df = 2; P < 0.0005), with this proportion lowest in May 2000. Less rigorous data on lactation status were available from 17 adult females captured in May 1999 in one trial area. Six of these were classified as 'lactating' by the veterinarians carrying out the necropsies, presumably on the basis of teat condition (see above).

Table 1 gives details of the cubs, and other possible mothers, captured at the same dens as the 37 actively lactating females and the six potentially lactating females. These data show that cubs likely to be the offspring of the culled females were captured in 31 of the 43 cases (5 in 1999, 3 in 2000, 10 in 2002, and 13 in 2003), suggesting that 12 litters were missed over the four years. There was no significant difference between years in the proportion of litters estimated to have been missed by culling operations (data from 2000–2003 only; $\chi^2 = 0.08$; df = 2; P = 0.96).

Where cubs were captured, the mean number of cubs per lactating female was 2.10 (\pm 1.19 SD). This is not significantly different from the average litter size at emergence recorded by field studies in roughly the same area (southwestern Britain; data from Neal & Cheeseman 1996: mean litter size is 2.36 \pm 0.83 SD; $t_{139} = 1.42$; P = 0.16). Thus, there is no evidence that incomplete litters were being captured. There was no difference between years in the number of cubs captured per lactating female (data from 2000–2003 only: $F_{223} = 0.35$; P = 0.71).

A reasonable estimate of the total number of cubs missed by culling operations can be obtained by assuming that the mean litter size estimated from field studies (2.36; Neal & Cheeseman 1996) was also the true mean litter size in trial areas. If this assumption is made, then the 43 actively lactating females culled across four years would have approximately 101 dependent cubs. A total of 65 were captured, suggesting that, on average, approximately nine cubs may have been missed by trapping operations each year.

The median date of capture for cubs was one day after the mother (inter-quartile range = 2.25 days, range = six days before to five days after). Of the 65 cubs captured in

^{© 2005} Universities Federation for Animal Welfare

Table I Females apparently lactating in May, with all cubs and possible alternative mothers captured at the same dens. 'Breeding status' refers to females' lactation status recorded at post mortem; note that females in active lactation were not distinguished from those with extended teats during 1999. Cubs were attributed to the most likely mother (or divided between potential mothers) according to their recorded lactation status. Superscripts indicate pairs of females caught at the same den.

Year	Cubs at same den	Alternative mothers at den (breeding status)	Cubs attributed to this mother
1999	3	0	3
	I	0	I
	6	l (lactating; see below) ^a	3
	6	l (lactating; see above) ^a	3
	5	0	5
	0	-	0
2000	4	0	4
	2	2 (teats extended)	2
	0	-	0
	I	0	I
2002	2	0	2
	I	0	I
	0	l (teats extended)	0
	I	0	I
	4	l (teats extended)	4
	0	0	0
	2	0	2
	0	l (teats extended)	0
	3	l (teats extended)	3
	0	0	0
	I	0	I
	2	0	2
	4	l (actively lactating, see below) ^b	2
	4	I (actively lactating, see above) ^b	2
2003	0	I (actively lactating, see below) ^c	0
	0	I (actively lactating, see above) ^c	0
	2	0	2
	I	I (actively lactating, see below) ^d	I
	I	I (actively lactating, see above) ^d	0
	0	0	0
	I	0	I
	2	0	2
	I	0	I
	0	0	0
	5	l (actively lactating, see below) ^e	3
	5	I (actively lactating, see above) ^e	2
	5	2 (teats extended)	5
	2	0	2
	0	0	0
	-	0	-
	· I	l (teats extended)	Ī
	I	0	I
	1	0	1

association with actively lactating females, 49 (75%) were caught either before, or up to two days after, capture of the presumed mother.

Discussion

The data presented here suggest that the number of cubs suffering starvation through culling of their mothers in the course of the field trial has been small. Between May 1999 and May 2003, the litters of 12 lactating females — approximately three per year on average — were estimated

to have been missed by culling operations. Taking into account the possibility that incomplete litters may have been captured on some occasions, if each lactating female is assumed to have had a litter of average size for the region (approximately 2.36 cubs; Neal & Cheeseman 1996), the total annual estimate of the number of dependent cubs orphaned by the culling operation is approximately nine per year.

The number of cubs missed by trial culling operations was substantially smaller than that projected and publicised by

24 Woodroffe et al

the NFBG. The trial design involves initial large-scale 'proactive' culling across ten trial areas, with follow-up culls in these areas intended to keep badger numbers low (Bourne et al 1998; Woodroffe et al 2003), as well as smaller-scale reactive culling, in response to TB outbreaks in cattle, in a further ten trial areas. The NFBG estimated that 2300 orphaned cubs would starve when initial culls were carried out (National Federation of Badger Groups 1999). The data presented here cover the period when all 10 initial proactive culls were carried out (they were completed in December 2002), as well as follow-up and reactive culls. While our estimates of the numbers of cubs missed are necessarily approximate, it seems very likely that the NFBG projection was highly inaccurate. One reason for the large discrepancy is that the NFBG estimate was based upon a distribution of the timing of births presented in Neal and Cheeseman (1996), which differs somewhat from the data used to formulate the closed season, showing a higher proportion of later births (in the period April-November). Neal and Cheeseman's data were accumulated largely by informal (albeit thorough) study, using a variety of techniques with varying reliability and with a strong possibility for over-representation of unusual cases. Their data therefore provide valuable information on the rare extremes of the breeding season, but are less useful for determining the true frequency distribution of badger births in Britain. The fact that so few actively lactating females were culled outside the closed season suggests that our estimates of birth and weaning dates were approximately correct.

Badger cubs will forage with their mothers (as well as with other badgers) in the period immediately following weaning. This raises the possibility that mothers which have recently ceased lactating might still have cubs that are, to some extent, dependent upon them. The extent of suffering that a cub would suffer if orphaned during this brief period is unknown, because observations of adults actively feeding cubs or helping them to forage are uncommon (Neal & Cheeseman 1996). However, since badgers feed on a wide array of prey items, none of which is likely to require specialist skills to capture, and since cubs are weaned at the time of year when food is most abundant, it seems likely that the degree of suffering would be less than that imposed on unweaned cubs. Unfortunately, it was not possible to evaluate the number of recently weaned cubs "missed" by culling operations, because it is not possible for staff carrying out necropsies to distinguish females that have recently stopped lactating from those that have lactated in previous years (Woodroffe 1992). Ongoing genetic studies will allow more reliable assignment of parentage and permit this kind of evaluation.

Interestingly, inter-annual variation in the proportion of females found to be still actively lactating in May (with this proportion lowest in May 2000) may be consistent with Woodroffe's (1995) finding that implantation occurs later in females which are thin in the autumn prior to implantation, ultimately associated with dry summers. Adult females captured in October 1999 (prior to the May 2000 lactation season) were significantly heavier (mean 10.9 ± 2.0 kg) than those captured in October 2002 (mean 9.9 ± 2.2 kg; $t_{467} = 4.49$; P < 0.0001; no data were available from October 2001 because of the FMD outbreak). This corresponds with higher summer rainfall in 1999 than in 2002 (total 320 mm versus 159 mm in July, August and September in southwestern UK [Meteorological Office 2003]).

As described above, the timing of the closed season was chosen to represent a balance between badger welfare and effective delivery of a candidate TB control policy. It is appropriate, therefore, to consider whether the length of the closed season should be altered to provide a better balance.

Adoption of the closed season had some practical disadvantages, since it limited the time available for badger culling and necessarily delayed responses to TB outbreaks in cattle (many of which are disclosed during winter when cattle are housed [Bourne et al 2000b]). At this stage of the trial, it is not known whether culling badgers in response to such cattle incidents can reduce the risk of further outbreaks in cattle. However, if such culling is effective, and if - as has been suggested (Krebs et al 1997) - rapid response improves this effectiveness, the reduction in the suffering of badger cubs afforded by the closed season comes at a cost. It is appropriate, therefore, to consider whether the length of the closed season could be reduced. Trial data cannot be used to evaluate the impact of shortening the closed season, since by definition no information could be gathered when culling was suspended. However, the data on timing of reproduction presented in Figure 2 suggest that shortening the closed season would lead to a marked increase in the number of cubs left to starve in the den. This suggests that reducing the length of the closed season would have serious welfare implications for badger cubs.

The effects of prolonging the closed season are more easily assessed. Extending the closed season into January would appear to have few benefits. No lactating females were culled in January during 2000-2003 (although 212 adult females were culled). For comparison, none of 49 females captured in Wytham Woods, Oxfordshire, in January 1991-1993 was found to be lactating (R Woodroffe, unpublished data). These data suggest either that very few females give birth in January, or that females with very small cubs rarely enter traps. In either case, culling in January would appear to have few welfare costs for newborn cubs. Extending the season into May could reduce the number of actively lactating females culled, although it would be impossible to eliminate entirely the risk of missing dependent cubs. Under the existing closed season, the number of unweaned cubs missed by culling operations is low (approximately nine per year), and substantially lower than predicted by the NFBG. We acknowledge that it is impossible to carry out a formal cost-benefit analysis, particularly while the effectiveness of badger culling in reducing the incidence of cattle TB remains unknown. Extending the closed season would compromise the speedy and effective implementation of badger culling as an experimental treatment and as a candidate TB control policy. TB

^{© 2005} Universities Federation for Animal Welfare

incidents in cattle can have serious economic consequences for farmers' livelihoods, may carry welfare costs for cattle, and raise public health concerns for farm workers. Given the need to develop an effective policy to alleviate these problems, as quickly as possible, we conclude that the length of the closed season is currently appropriate. However, since (as discussed above) badgers' birth dates vary between years in response to environmental conditions, we propose to continue evaluation of the closed season's performance throughout the course of the field trial, and to modify it in future if necessary.

Acknowledgements

All of the data presented here were provided by staff of the Department for Environment, Food and Rural Affairs' Wildlife Unit, and the Veterinary Laboratories Agency, to whom we extend our thanks. The manuscript was improved by comments from three anonymous reviewers.

References

Bourne J, Donnelly C, Cox D, Gettinby G, Morrison I and Woodroffe R 1998 Towards a Sustainable Policy to Control TB in Cattle — A Scientific Initiative. Ministry of Agriculture, Fisheries and Food: London, UK. Available at http://www.defra.gov.uk/ animalh/tb/isg/isgrep1.htm

Bourne J, Donnelly C, Cox D, Gettinby G, Morrison I, McInerney J and Woodroffe R 2000a Bovine tuberculosis: towards a future control strategy. Veterinary Record 146: 207-210 Bourne J, Donnelly C, Cox D, Gettinby G, Morrison I, Woodroffe R and McInerney J 2000b An Epidemiological Investigation into Bovine Tuberculosis. Department for Environment, Food and Rural Affairs: London, UK. Available at http:// www.defra.gov.uk/animalh/tb/publications/index.htm

Canivenc R, Bonnin M and Ribes C 1981 Déclenchment de l'ovo-implantation par allongement de la phase sombre de la photopériode chez le Blaireau européen *Meles meles* L. *Comptes Rendues de l'Academie de Science de Paris Série III 292*: 1009-1013 [Title translation: Early implantation induced by experimental lengthening of the dark phase of photoperiod in the European badger *Meles meles* L]

Creel SR, Monfort SL, Wildt DE and Waser PM 1991 Spontaneous lactation is an adaptive result of pseudopregnancy *Nature 351*: 660-662

Dumartin B, Ribes C, Souloumiac J, Charron G and Canivenc R 1989 Determination experimentale de la croissance foetale chez le blaireau européen *Meles meles L. Mammalia 53*: 279-285 [Title translation: Experimental determination of foetal growth rate in the European badger *Meles meles* L]

Ewbank R 2003 Second Independent Audit on the Humaneness of Badger Despatch. Product code PB 8253. Department for Environment, Food and Rural Affairs: London, UK. Available at http://www.defra.gov.uk/animalh/tb/publications/index.htm

Kirkwood JK 2000 Humaneness of MAFF's Badger Despatch Procedures. Ministry of Agriculture, Fisheries and Food: London, UK. Available at http://www.defra.gov.uk/animalh/tb/ publications/auditor/report.htm

Krebs JR, Anderson R, Clutton-Brock T, Morrison I, Young D, Donnelly C, Frost S and Woodroffe R 1997 Bovine Tuberculosis in Cattle and Badgers — An Independent Scientific Review. Her Majesty's Stationery Office: London, UK

Kruuk H 1989 The Social Badger. Oxford University Press: Oxford, UK

Meteorological Office 2003 *UK Climate and Weather Statistics.* Met Office: Exeter, UK. Available at http://www.metoffice.gov.uk/ climate/uk

National Federation of Badger Groups 1999 Badgers and Bovine Tuberculosis. Submission to the House of Commons Agriculture Committee. National Federation of Badger Groups: London, UK. Available at http://www.badgers.org.uk/nfbg/tb

Neal E and Cheeseman C 1996 Badgers. Poyser: London, UK Neal EG and Harrison RJ 1958 Reproduction in the European badger (Meles meles L.). Transactions of the Zoological Society of London 29: 67-131

Page RJC, Ross J and Langton SD 1994 Seasonality of reproduction in the European badger *Meles meles* in south-west England. *Journal of Zoology 233*: 69-91

Smith GC, Cheeseman CL and Clifton-Hadley RS 1997 Modelling the control of bovine tuberculosis in badgers in England: culling and the release of lactating females. *Journal of Applied Ecology* 34: 1375-1386

Tuyttens FAM, Delahay RJ, Macdonald D, Cheeseman CL, Long B and Donnelly CA 2000 Spatial perturbation caused by a badger (*Meles meles*) culling operation: implications for the function of territoriality and the control of bovine tuberculosis (*Mycobacterium bovis*). Journal of Animal Ecology 69: 815-828 Tuyttens FAM, Macdonald DW, Delahay R, Rogers LM,

Mallinson RJ, Donnelly CA and Newman C 1999 Differences in trapability of European badgers *Meles meles* in three populations in England. *Journal of Applied Ecology* 36: 1051-1062

Woodroffe R 1992 Factors affecting reproductive success in the European Badger, Meles meles L. PhD Thesis, University of Oxford, UK

Woodroffe R 1993 Alloparental behaviour in the European Badger. *Animal Behaviour* 46: 413-415

Woodroffe R 1995 Body condition affects implantation date in the European badger, *Meles meles. Journal of Zoology* 236: 183-188 Woodroffe R and Macdonald DW 2000 Helpers provide no detectable benefits in the European badger, *Meles meles. Journal of Zoology* 250: 113-119

Woodroffe R, Bourne FJ, Donnelly CA, Cox DR, Gettinby G, McInerney JP and Morrison WI 2003 Towards a sustainable policy to control TB in cattle. In: Tattersall F and Manley W (eds) Conservation and Conflict: Mammals and Farming in Britain. Linnean Society: London, UK