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Badger (*Meles meles*) as a model species for the development of ecological and behavioural research

Jezevec lesní (*Meles meles*) jako modelový druh pro rozvoj ekologického a behaviorálního výzkumu

Pavel STOPKA[1, 2] & Dominic D. P. JOHNSON[2]

[1] Biodiversity Research Group, Department of Zoology, Charles University, Viničná 7, CZ–128 44 Praha 2, Czech Republic
[2] Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, United Kingdom

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Abstract. Pilot studies of KRUUK (1989) in the UK revealed that amongst Mustelidae badgers are unusual as they form large groups sharing a communal site. Although there is a profusion of studies on badgers from the UK, there is genuine lack of supporting evidence that they are particularly social elsewhere in Europe, and densities are extremely variable. Such great geographic variation in behaviour provides an excellent opportunity to progress in testing models of social behaviour and cooperation in mammals. This area of research is also important because in Britain badgers have been linked to the spread of bovine tuberculosis. Whether this is likely to be a problem elsewhere in Europe largely depends on understanding the ecology and behaviour of badgers and their interactions with other mammalian species. The aim of this paper is to highlight the recent developments in the study of the social biology of this species, with a view to encouraging more research in Europe.

ECOLOGY AND SOCIO-ECOLOGY OF BADGERS

The accumulating number and geographical spread of studies on badgers, *Meles meles* (Linneaeus, 1758) (GRIFFITHS & THOMAS 1993, JOHNSON et al. in press [a], KOWALCZYK et al. in press) is allowing ever more powerful comparative tests of a number of important biological hypotheses. From the point of view of ecological and behavioural hypotheses, however, there remains a significant bias in the disproportionate amount of literature from the British Isles. The long-term studies carried out there have enabled some very detailed studies of, for example, population dynamics, epidemiology and social behaviour (MACDONALD et al. 1996, submitted, ROGERS et al. 1998, TUYTTENS et al. 1999). In this section we make a case for the great importance of new information from sites across the rest – by far the majority – of the badger's geographic range.

The Atlantic climate of the British Isles is certainly not representative of most of the badger's distribution and indeed many aspects of their behavioural ecology in that country have been attributed to the unusual climate (DA SILVA et al. 1993, JOHNSON et al. in press [a], KRUUK 1978a, KRUUK & PARISH 1981, KRUUK et al. 1979). There is enormous ecological variation across the badger's range, from dry desert regions such as Jordan in the

Middle East (Neal & Cheeseman 1996) to strongly seasonal Scandinavian environments such as Norway (Brüseth et al. 1997), and from the mild agricultural landscape of England (Kruuk 1989), to the ancient forests of Poland (Kowalczyk et al. in press). In comparison to this diversity of ecological conditions, the climate and vegetation within the British Isles varies very little, and consequently the statistical power of using ecological variables to explain variation in social spacing behaviour and life-histories within that region is also relatively low. Analyses of different badger populations between geographic regions provide, therefore, especial opportunities for empirical tests of theory in two particular areas of ecology, discussed below.

Firstly, there are few large mammal species for which detailed information is known from enough sites to make informative tests of biogeographic hypotheses about life-history variation. Badgers have a good opportunity to become an exception, because there is now an increasing number of reports – though more are still clearly needed – from new study sites across the continent which is gradually building up a detailed spatial data set in the literature of various population and biometric parameters. This is accumulating an invaluable record of intra-specific variation. Such comparative data has led to the possibility of specific tests of biogeographic hypotheses (Virgos & Casanovas 1999) with reasonably large sample sizes (Johnson et al. in press [a], Kowalczyk et al. in press). Furthermore, traditional views on geographic variation in environmental variables leading to adaptive intra-specific variation in animals have recently been challenged (see Gortazár et al. 2000). Badgers provide an ideal model for tests of such comparisons, for instance those of short-term changes in body size variation, as well hypotheses about inter-specific competition and niche separation (Dayan & Simberloff 1994, Lynch et al. 1997, Pelikán & Vackar 1978). The fact that Badgers utilise visible setts throughout their geographic range provides relatively easy opportunities to make assessments of occurrence, habitat and sett-site selection preferences (Biancardi & Rinetta 1988, Matyáštík & Bičík 1999); these do not require equipment and can be made over short time scales, but nevertheless provide invaluable information (Macdonald et al. 1996).

The second major area to which badger studies have and should continue to make an important contribution is in theories of sociality and group size variation in mammals. Badgers already played central role in providing tests of hypotheses for social grouping in animals (Woodroffe & Macdonald 1993, 2000). Early work by Hans Kruuk in Wytham Woods (Kruuk 1978a, b) led to the development of now widely debated hypotheses of social group formation which have been extended to the Carnivora in general (Carr & Macdonald 1986, Macdonald 1983, Macdonald & Carr 1989). One of these, the RDH, has since gained support from mathematical modelling (Bacon et al. 1991) and tests of predictions have been made in some populations (Brüseth et al. 1997, Johnson et al. in press [b]). However, preliminary investigations suggest that more powerful analyses of the same hypotheses may be yet to come from inter-population comparisons (Johnson et al. in press [a], submitted). Therefore, the resolution of whether, and to what extent, such hypotheses do predict social behaviour of badgers (and other mammals in general) is likely to come at least in part from comparisons made between populations.

SOCIAL BIOLOGY OF BADGERS

The behaviour of the European badger has mostly been studied in the UK where at some places the population densities are particularly amenable for studying social behaviour

among individuals living in groups of different sizes. Differences in population densities across their geographic distribution may result in different mating systems. Originally, KLEIMAN (1977) described badgers as facultative monogamists but more recent studies from the UK revealed that even relatively low densities of badgers can result in multi-individual social structures (WOODROFFE & MACDONALD 1993) which, therefore, does not support the argument for monogamy in this species. Indeed sperm competition is being shown to occur in a great many mammalian species (MÜLLER & BIRKHEAD 1989), so even apparent behavioural monogamy (i. e. pair-living) may be misleading. Some studies from Europe suggest badgers are not strictly monogamous (REVILLA & PALOMARES 1999), but it strikes us that, to our knowledge, there is a singular lack of information specifically about the mating systems of different badger populations across Europe. MACDONALD's (1983)

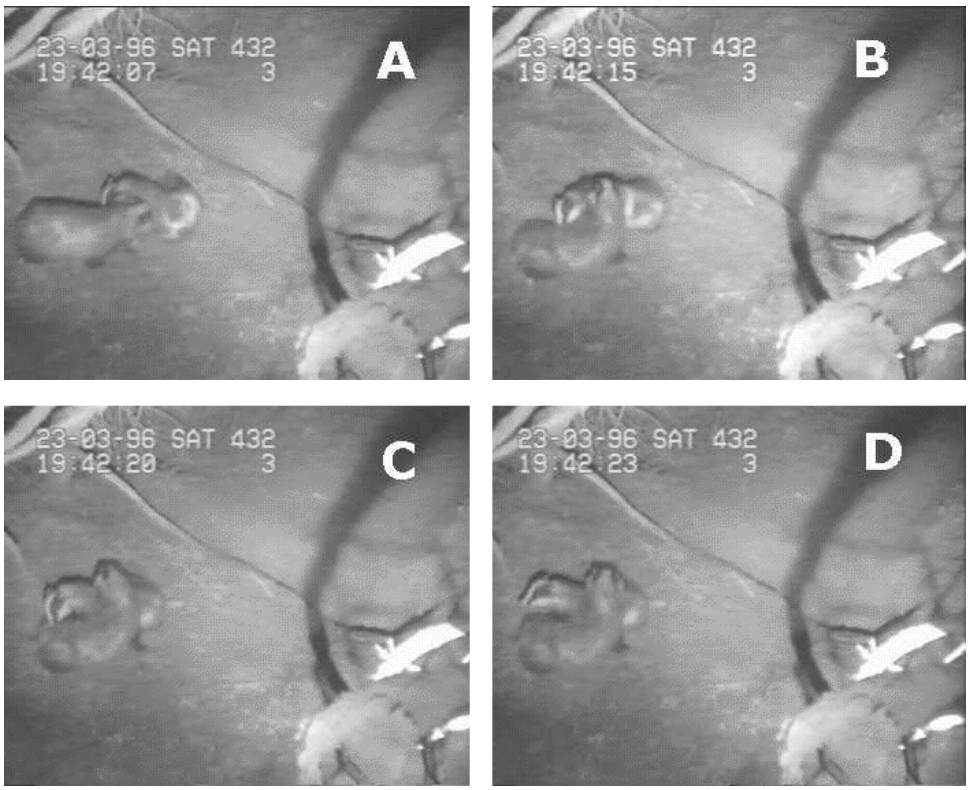

Fig. 1. A time-sequence sample of a grooming interaction in badger. Individual badgers groom in a simultaneously reciprocal fashion using a generous 'tit-for-tat'-like rule set, that ensures similar durations of grooming are given and received (STEWART 1997). Interaction is usually ended when one of the individuals stops allo-grooming an opponent (picture D).
Obr. 1. Příklad kooperativního odstraňování ektoparasitů (allogrooming) u jezevců v čase. Jezevci kooperují recipročně strategií známou jako "tit-for-tat". Ta umožňuje, aby čas vynaložený na vydaný allogrooming přibližně odpovídal allgroomingu přijatému u obou jedinců. Tato sociální interakce je obvykle ukončena, pokud jeden z účastníků neopětuje allogrooming během několika sekund (viz D).

suggestion that badgers form non-cooperative social groups defending a common territory because of the spatio-temporal pattern of food availability means groups may form without any functional benefits of group-living. However, group marking at latrine sites and object marking behaviour already suggests some form of cooperation operates in this species, in that this form of communal 'defence' reveals a stable pattern for at least mating season. Recently, STEWART (1997) studied cooperation based on allogrooming behaviour in badgers, in which individuals groom each other in a simultaneously reciprocal fashion using a generous 'tit-for-tat'-like rule set, that ensures similar durations of grooming are given and received. Despite these interesting developments which suggest badgers are a very useful model for studying cooperation at different levels of resolution (MACDONALD et al. 2000), studies on whether they cooperate or not have, to date, concentrated on correlational analyses of returns for assumed cooperation (WOODROFFE 1993, WOODROFFE & MACDONALD 2000), or operate from the starting assumptions that cooperation is absent (WOODROFFE & MACDONALD 1993). Detailed analyses of behavioural interactions are needed (see Fig. 1), however, to evaluate accurately fitness consequences of such cooperation at different levels of time resolution (STOPKA et al. in press).

Techniques to achieve these more detailed analyses have been developed in Wytham (STEWART et al. 1997) and have revealed aspects of behaviour which had until now not been possible to uncover. For example, detailed analysis of agonistic behaviours revealed that, very unusual for most social mammals, badger groups are not organised in dominance hierarchies (MURPHY et al. in press). This is particularly interesting in the light of earlier assumptions that they did exist (WOODROFFE & MACDONALD 1995), and the field observation experiments that failed to distinguish hierarchies (MACDONALD et al. in prep). Detailed analyses were, in this case, required to illuminate behaviours that are crucial for understanding social organisation.

Although large groups share underground dens called setts, additional setts – known as outliers – are often built outside of the main setts. There are differences in the extent that individual badgers maintain these setts and excavate new entrances. Furthermore, those individuals which invest most effort are often those which are most likely to gain reproductive benefits from a well maintained or enlarged sett (MACDONALD et al. 2000). BUTLER & ROPER (1996) tested the hypothesis that setts allow badgers to move between different sett chambers to avoid increased ectoparasite loads. As the badger species-specific flea *Paraceras melis* moves frequently between badgers and reacts to carbon dioxide (COX et al. 1998) by which it detects an animal, the optimal way of avoiding this burden is to enlarge current setts or to build new ones. Understanding the dynamics of such ectoparasites and the host specific responses is also important in estimating the role fleas play in transmitting various micro-parasites such as *Trypanosoma* and *Babesia* (ANWAR et al. 2000, MACDONALD et al. 1999), where the latter can be lethal.

CONCLUSIONS

In order to further the understanding of sociality and the evolution of social behaviour in mammals – including humans – good model species are needed to test predictions of various generic models of evolution.

The great geographic variation in the ecology and social organisation of badgers makes them a perfect model species to test such predictions.

There remains, however, a bias towards studies of badgers from the UK, which is not representative of the majority of the badger's range. Therefore, studies from elsewhere are vital to resolving issues surrounding the evolution of social behaviour from the comparative point of view.

One of the advantages of the in-depth studies from the UK is that methodologies and approaches for obtaining the necessary data are well developed.

The relevance of all of these points is greatly increased at present because of the badger's role in the spread of bovine TB. Understanding the mechanisms and dynamics of social behaviour in badgers is critical to its control.

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SOUHRN

Jeden z prvních výzkumů jezevců ve Velké Británii (Kruuk 1989) odhalil, že tito savci – v rámci celé čeledi Mustelidae – vytvářejí neobvykle velké sociální skupiny a společné podzemní nory (tzv. hrady). Z území Velké Británie existuje řada studií na toto téma, dosud však nebylo prokázáno, že by jezevci žili sociálně i na jiných místech Evropy, ačkoliv bylo známo, že se hustota populací jezevců v různých oblastech velmi liší. Takto daná potenciální rozmanitost v možnostech sociálního uspořádání tak poskytuje příležitost pro testování modelů sociálního chování a kooperace. Výzkum jezevců je důležitý také z toho důvodu, že byla ve Velké Británii zjištěna souvislost mezi počtem a mobilitou jezevců a šířením tuberkulózy domácího skotu. Studium a pochopení této problematiky může napomoci jejímu řešení, a to i v případě výskytu tohoto onemocnění i mimo území Velké Británie. Cílem tohoto příspěvku je vyzdvihnout současný vývoj studia sociální biologie jezevce lesního se záměrem podpořit obdobný výzkum v kontinentální Evropě.

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