

Why are group-living badgers (*Meles meles*) sexually dimorphic?

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Abstract

One of the hypotheses proposed to account for why badgers *Meles meles* are highly social in the U.K., the resource dispersion hypothesis, is that patchy resources are unpredictably dispersed in the environment and therefore must be shared, but that these patches are rich enough, when available, to support several badgers at any one time. Previous empiricists in our study site at Wytham Woods calculated that single patches could be rich enough to support 30 badgers in a night. The sustained increase in population density in Wytham Woods suggests that food was not limiting and territories were below capacity, and therefore that feeding competition was relatively low. Low feeding competition would predict an absence of dimorphism in trophic apparatus between the sexes. Contrary to this, significant sexual dimorphism was found, after removing effects resulting from body size allometry, in canine cross-section length, width (both $P < 0.0001$) and skull breadth ($P < 0.001$). The differences in canine dimensions were still significant when allometry of both body length and skull breadth are accounted for statistically ($P < 0.0001$). It is therefore suggested that feeding competition may not necessarily be low, which would have implications for understanding the costs of social behaviour. Alternative explanations involving sexual selection and phylogenetic inertia are discussed.

Key words: *Meles meles*, badgers, sexual dimorphism, canines, allometry, group-living

INTRODUCTION

The 'resource dispersion hypothesis' (RDH; Macdonald, 1983; Carr & Macdonald, 1986; Macdonald & Carr, 1989; Bacon, Ball & Blackwell, 1991*a,b*), proposes that solitary foragers, such as badgers *Meles meles*, may form spatial groups passively around patchy resources in the environment rather than exploiting any functional benefits of group living. There are many facets to the hypothesis, but the principal prediction is that resource patches within a territory may be rich enough over a given time to sustain the nutritional requirements of more than a primary pair of individuals. Studies have supported the RDH in demonstrating that the distribution and richness of patches of habitat rich in earthworms (the main food of badgers; Kruuk, 1978*a*) correlate with social organization and aspects of group structure (Kruuk, 1978*b*; Kruuk & Parish, 1982; Hofer, 1988; Da Silva, 1989; Da Silva, Woodroffe & Macdonald, 1993; Woodroffe & Macdonald, 2000). In

particular, earlier studies in Wytham Woods have found that when available (which depends on certain weather conditions) earthworm patches can offer extraordinarily abundant resources. On the basis of energetic calculations, Kruuk (1978*a*) suggested that a single patch of pasture could provide the demands of up to 30 badgers in one night. While such large groups do occur (Da Silva *et al.*, 1993), mean adult group sizes, even in the high density populations, are typically much lower than this (Woodroffe & Macdonald, 1993; Neal & Cheeseman, 1996) implying that food is in relative abundance. Although it is periods of low rather than high food availability that limit densities, the fact remains that by some mechanism (while not necessarily the RDH) group sizes are uncharacteristically large for the species in the agricultural woodland mosaics of southern England and, moreover, these groups occupy very small territories (Johnson, Macdonald & Dickman, 2000), leading to some of the highest reported densities anywhere. Of course, even very rich territories must eventually reach carrying capacity. However, the great population density increase in Wytham over the last 3 decades (Kruuk, 1978*b*; Newman, 2000) suggests that food has not been limiting and territories were well below

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carrying capacity. Rather, it is suggested that social factors have maintained the population below carrying capacity (Newman, 2000).

If carrying capacity has not been reached, competition should be relatively low. One prediction of low levels of feeding competition is that sexual differentiation in feeding apparatus (to enable inter-sexual niche separation) is small (Dayan & Simberloff, 1996). We tested this hypothesis in a population of group-living badgers in Wytham Woods.

Detailed studies of sexually dimorphic traits are also important because for most species, and mustelids in particular, the principal driving factor behind sexual dimorphism remains to be distinguished. The many hypotheses for size differences between the sexes in mustelids have recently been reviewed by Dayan & Simberloff (1996, 1998). For example, males may be selected for larger body size to attain dominance over other individuals, and to cover a greater range in search of females (Erlinge, 1979; Moors, 1980). On the other hand, Erlinge (1979) and Moors (1980) argued that females have lower total energy demands if they are smaller (20% less than a hypothetical female of male-size) and can therefore 'channel more energy into reproduction' (Moors, 1980: 147). This hypothesis was supported using a model based on field data (Powell & Leonard, 1983). Sandell (1989) also concluded (using energetic arguments) that sexes should have a different optimum mass during the breeding season. Smaller females may also benefit by having access to smaller prey-burrows than do males, or being small enough to fit down the same burrows when pregnant (Gliwicz, 1988). In general then, there are two principal and unresolved hypotheses for sexual dimorphism: (1) inter-male mating competition (Erlinge, 1979; Moors, 1980); (2) inter-sexual food exploitation competition (Brown & Lasiewski, 1972).

In many mammals, inter-male competition and asymmetries in male reproductive success lead to enormous morphological differences between the sexes (Trivers, 1972; Cox & LeBoeuf, 1977; Lincoln, 1994). Male size dimorphism has been shown to correlate with the intensity of inter-male competition (Clutton-Brock, Harvey & Rudder, 1977) and polygynous mammals show greater sexual dimorphism than monogamous ones (Ralls, 1977). However, sexual dimorphism specifically in trophic structures (i.e. assumed to be due to inter-sexual food exploitation competition) has now been documented in a very wide diversity of taxa from across the animal kingdom (Shine, 1989). Furthermore, Shine (1989) argued that while the inter-male competition hypothesis has generally become accepted as the principal explanation for sexual size dimorphism, this has been done with no better reason than parsimony, and that the hypothesis has more easily testable predictions, leading to more publications. This disparity has arisen because of the complexity of testing the inter-sexual food exploitation competition hypothesis, which can only be demonstrated by showing that: (1) dimorphism in trophic structures is greater than

expected by allometry (i.e. over and above gross differences in body size); (2) that it is not the result of sexual selection (Selander, 1972). These criteria may be overly strict however, since allometry may secondarily follow trophic adaptation if there is no opposing selection, and sexual selection may simultaneously be selecting for larger body size (Shine, 1989).

Slatkin (1984) used a model to show that sexual dimorphism could evolve as a result of ecological factors alone. However, a major problem of the food exploitation competition hypothesis is that it predicts no direction in dimorphism, so that it would have been expected that females would be the larger sex in 50% of species. Because it is only ever males that are larger, the food exploitation competition hypothesis cannot be an exclusive explanation. It has been suggested as probable, therefore, that among many species male-male sexual competition initiates a dimorphic size trend and, once in place, the potential advantages of niche separation reinforce the displacement (Slatkin, 1984; Hedrick & Temeles, 1989; Shine, 1989).

Nevertheless, securing evidence that ecological factors are responsible for sexual dimorphism has been plagued with difficulties, and results have often been contradictory. For example, while some empirical studies in mustelids have failed to identify sexual differences in niche breadth or character displacement (Erlinge, 1979; Moors, 1984; Ralls & Harvey, 1985) others did find such differences (Birks & Dunstone, 1985; Dayan & Simberloff, 1996) and that, across mustelids in general, there is a general tendency for females to exploit smaller prey than males (Moors, 1980). More recently, evidence has emerged of specific character displacement in European otters *Lutra lutra* (Lynch, Conroy, *et al.*, 1996), and in canine diameter across the mustelid-viverrid guild in Israel and weasels *Mustela nivalis* in North America (Dayan *et al.*, 1989) and mustelids in the British Isles (Dayan & Simberloff, 1994). In the course of the development of this area of research, canines have been championed as a better indicator of trophic selection than commonly used measures like condylobasal length and body mass, because canines are functionally associated with killing and feeding in carnivores (Dayan *et al.*, 1989; Dayan & Simberloff, 1994; Biknevicius & Van Valkenburgh, 1996; Dayan & Simberloff, 1996, 1998). Certainly, it is clear from the various contradictory findings outlined above that selection of the ecologically relevant variables is critical to the resolution of this problem.

A further problem is that many previous studies of sexual dimorphism have been confounded because they do not take account of the fact that variation in overall body size must be removed to show that dimorphisms in other structures are significant over and above that expected by the difference in body size alone (*sensu* Shine, 1989). Studies on skull collections, in particular, cannot easily resolve this problem. We specifically demonstrate here clear sexual dimorphism in canine size over and above residual differences in overall body and skull proportions, which is the only way to begin to

tease apart any interactive effects of the two different hypotheses for sexual dimorphism (Selander, 1972; Shine, 1989). This study therefore has three specific advantages: (1) we use live badgers which allowed us to measure and remove body length as a covariate indexing skeletal size; (2) we focus on a trophic structure; (3) sexual dimorphism in this population has until now not been explicitly examined, yet the evaluation of the different hypotheses for sexual dimorphism has important consequences for understanding their social behaviour.

METHODS

Study site

Badgers came from a long-term study in Wytham Woods, 10 km north-west of Oxford (01°18'W, 51°46'N). Details of the study site can be found in Hofer (1988) and Kruuk (1978a), and of the long-term trapping study in Tuytens *et al.* (1999).

Badger sample

Trapping studies have been conducted since 1974 and follow the methodologies of previous studies in this population (Kruuk, 1978b; Hofer, 1988; Da Silva, 1989; Tuytens *et al.*, 1999; Newman, 2000). Badgers for this sample were trapped under licence during 1998 near their setts and individually marked, using standard methods (Cheeseman & Harris, 1982). Only 1998 data were used because canine measurements have only been taken during this period for the first time. Badgers were anaesthetized with ketamine (Vetalar, Park Davies) before taking biometric data, and then released the same morning at the same location where they were trapped.

Biometric measurements

Canines were measured in adults only, using callipers to a 0.01-mm level of accuracy. We measured the antero-posterior length (the maximal length, anterior to posterior, of the cross-section) of the upper left (ULCL) and upper right (URCL) canines at the point where they meet the gums, and the mediolateral breadth (the width of this cross-section; ULCW and URCW). We measured body length from the tip of the nose to the base of the pelvis while lying flat, ventral side up (to 5 mm) using a metre rule. Zygomatic arch width and rear left pastern length were measured with callipers (to 1 mm). Body mass was measured with a spring balance to 0.1 kg. Body condition and tooth wear were assessed on an ordinal scale of 1–5.

Measurement error was assessed using repeat measurements on 2 badgers which were recaptured 8 days later, and had a median of 0.15 and 0.16 mm

for canine length and width, respectively. Although 2 recaptured badgers should have given 8 measures to compare (2 × 4 possible measures: ULCL, URCL, ULCW, URCW), the upper right canine in 1 badger was lost between captures. Thus 6 measures were compared, and combined to give 1 error estimate for canine width and 1 for canine length ($n = 3$ for both).

No outliers were omitted from any of the analyses, and no individual was included more than once in the data. Sex differences in dependent variables were tested for using *t*-tests for a single variable, and analysis of covariance (ANCOVA) when removing variation resulting from a second, continuous explanatory variable.

RESULTS

Significant differences between the sexes were found in upper left canine cross-section length ($F_{2,48} = 42.559$, $P < 0.0001$; Fig. 1a) and width ($F_{2,46} = 40.031$, $P < 0.0001$; Fig. 1b), using ANCOVA to remove body length as a covariate. Body length itself was a non-significant variable in both models ($P = 0.29$ and $P = 0.11$, respectively). Upper right canine measurements were significantly predicted by those of the upper left canines (length, $F_{1,45} = 194.248$, $P < 0.0001$, $r^2 = 0.81$; width, $F_{1,43} = 95.863$, $P < 0.0001$, $r^2 = 0.69$, so these were not tested separately. We removed body length as this provides an index of skeletal size. However, when body mass was removed rather than body length, canines were also significantly sexually dimorphic in cross-section length ($F_{2,49} = 46.453$, $P < 0.0001$) and width ($F_{2,47} = 45.368$, $P < 0.0001$).

There was significant sexual dimorphism in body length ($t_{60} = 2.72$, $P = 0.008$), but no significant difference in tooth wear or body condition between the sexes (*t*-tests, $P > 0.06$ for both). Once body length was again removed as a covariate, there was no significant sexual dimorphism in body mass ($F_{2,59} = 0.356$, $P = 0.55$) or rear left pastern length ($F_{2,42} = 0.298$, $P = 0.59$). However, the zygomatic arch width was still significantly larger in males after body length was removed ($F_{2,59} = 8.036$, $P = 0.006$). Removing zygomatic arch width alone, instead of body length, canine cross-section length and width were still both significantly different between the sexes (length, $F_{2,48} = 34.732$, $P < 0.0001$; width, $F_{2,46} = 32.296$, $P < 0.0001$). Lastly, even when both body length and zygomatic arch width were removed as a covariate, there was still a highly significant sexual dimorphism in both upper canine cross-section length ($F_{3,47} = 33.157$, $P < 0.0001$) and width ($F_{3,45} = 30.227$, $P < 0.0001$).

DISCUSSION

We have demonstrated that badgers exhibit significant sexual dimorphism in feeding apparatus, over and above sex differences in body and skull size. This difference was highly significant for both canine cross-

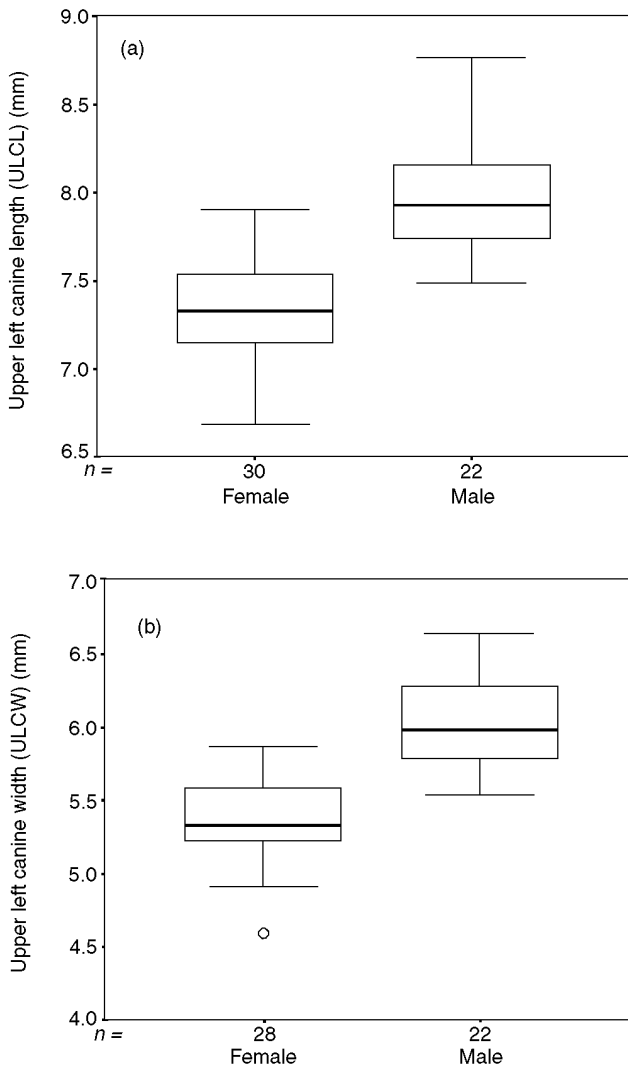


Fig. 1. Sexual dimorphism in canine cross-section length (a) and width (b). Box, inter-quartile range; line, median; whiskers, highest and lowest values, excluding outliers; open circles, outliers 1.5–3 box lengths from the inter-quartile range.

section length and canine cross-section width, after removing the confounding effects of either body size allometry (indexed by body length) or skull size, or both of these variables together. In addition, it is notable that the zygomatic arch width was also significantly sexually dimorphic (again after removing variation resulting from body length) given that the size of this structure is an index of the power of the temporalis muscle used in jaw closure (Biknevicius & Van Valkenburgh, 1996).

Such differences in feeding apparatus indicate some level of selection for niche separation between the sexes (Dayan & Simberloff, 1996). One conclusion is, therefore, that feeding competition may indeed be an important selective pressure in current populations. There is some evidence to support this. Although earthworms may compose up to 90% of the diet during

certain times of the year in Wytham (Hofer, 1988), there are periods in the summer when the hardened earth makes earthworms difficult to obtain, and at these times of year badgers are forced to use other food sources. Birds and mammals are not uncommonly found in the diet of British badgers (Neal & Cheeseman, 1996), which further suggests that the dental apparatus may still be under some selective pressure to enable the killing, or processing, of prey. In addition, the significant density-dependent effects on body condition and weight as well as high cub mortality in very dry summers (Newman, 2000) may suggest that feeding competition is certainly, at the least, not negligible in our population. Density-dependent effects on body weight and fecundity have also been reported in other high-density populations (Cresswell *et al.*, 1992; Rogers, Cheeseman & Langton, 1997).

One problem with using canines as a measure of trophic differentiation is that, in many mammals, they are also used in threat displays and for fighting (Lincoln, 1994). However, Dayan & Simberloff (1996, and references therein) have concluded that sexual selection for enlarged canines is unlikely to be important in badgers, and mustelids in general, because fighting over females and threat displays are relatively rare. These authors also point out that species of Canidae, which commonly bare canines in ritualized behaviours, nevertheless exhibit clear character displacement in canine size (Dayan & Simberloff, 1996) as do the community of mustelid species in the U.K. (Dayan & Simberloff, 1994). The competitive advantages of male sexual dimorphism may be small in multi-male social groups because females may deny any certainty of paternity to males, through frequent and diverse mating. This latter conjecture is supported by at least four lines of evidence: (1) our unpublished observations of badgers indicate very little overt male–male aggression over females when consorting and mating; (2) the most social species (European badger, sea otter *Enhydra lutris*, giant otter *Pteronura brasiliensis*, striped skunk *Mephitis mephitis* and spot-necked otter *Lutra maculicollis*) all have relatively low sexual dimorphism in body mass (Johnson *et al.*, 2000); (3) the European otter *Lutra lutra* in Shetland, where it is particularly social, has a lower cranial and dental sexual dimorphism than within populations of conspecifics elsewhere (Lynch, Conroy *et al.*, 1996); (4) an independent contrasts analysis across all mustelid species detected no correlation between breeding group size and sexual dimorphism (Johnson *et al.*, 2000). Overall, although the use of canines in fighting or threat displays cannot be ruled out, it seems to be an unlikely or only partial explanation for our results. To quote Dayan & Simberloff (1996: 260), ‘it is unlikely that evolution would have calibrated canine size differences among mustelids in response to this selective pressure’.

Although we could therefore tentatively conclude that the significant sexual dimorphism in these trophic structures has been selected for as a result of feeding competition, it is still uncertain when that selective

pressure occurred, and therefore whether it still applies. Even though we provided some contemporary evidence in support of the idea that current feeding competition may not be as low as suggested by our initial observations of population increases and dispersion of rich food patches, sexual dimorphism may have remained as a vestigial trait selected for in ancestral populations which experienced more intense feeding competition in the past. This problem has, as far as we could tell, not featured in the literature surrounding this topic, yet it could explain the absence of evidence for niche separation despite trophic dimorphism in certain contemporary communities. For badgers, this seems a compelling possibility, given that population densities are much lower in all other areas across Europe where the badger has been studied (Kowalczyk, Bunevich & Jedrzejewska, 2000), which is likely to be due in part to food constraints (Goszczynski *et al.*, 2000; Johnson *et al.*, 2000). Indeed, it is the unusually high abundance of earthworms in the modern agricultural landscape that is held to be the primary factor permitting such high densities of badgers in the U.K. (Kruuk, 1978*a,b*; Kruuk & Parish, 1981, 1982; Ashby & Elliot, 1983; Hofer, 1988; Da Silva *et al.*, 1993; Roper, 1994). Elsewhere, badgers seem to adapt to a variety of different prey. A recent review (Goszczynski *et al.*, 2000) suggests that the biogeographic variation in earthworm availability is primarily responsible for determining badger diets, which vary considerably. There may be a basis for inter-sexual niche separation and character displacement where badgers have more specialist diets, such as rabbits *Oryctolagus cuniculus* in Spain (Martín, Rodríguez & Delibes, 1995) and insects and fruits in Italy (Kruuk & De Kock, 1981; Pigozzi, 1988). Since badgers arrived in the U.K. only relatively recently (Neal & Cheeseman, 1996), we may be observing sexual dimorphism selected for in a previous era under different conditions but which has not been selected out again.

For badgers, if the explanation of sexual dimorphism is indeed that of feeding competition, then one would predict dimorphism in trophic structures to correlate with the degree of competition. Data on geographic variation in canine size and other trophic structures, along with data on the degree of competition (indexed by group sizes or densities) are needed to test this. Other studies have been successful in showing inter-population differences in other craniometric features of badgers (Lynch, Whelan *et al.*, 1997; Harmsen & Van Bree, 1998) as well as inter-population diet variation (Goszczynski *et al.*, 2000). The great diversity of badger social organization across Europe seems to provide a perfect opportunity to test this hypothesis.

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