CHAPTER 13

Asian badgers—the same, only different: how diversity among badger societies informs socio-ecological theory and challenges conservation

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There are 11 badger species occurring across Asia. The Chinese ferret badger (*Melogale moschata*), shown here, is especially interesting because, in our study, they live in groups. Photo taken in the Houhe National Nature Reserve, Hubei Province, China.© Youbing Zhou

Introduction

Understanding what factors drive conspecifics to congregate, and ultimately to establish groups, is central to socio-ecology (Alexander 1974; Smith et al. 2012; Macdonald and Johnson 2015). Under particular environmental conditions, such as the concentration of food (Macdonald 1983; Carr and Macdonald 1986; Creel and Macdonald 1995; Johnson et al. 2000), multiple individuals are drawn into (or remain in, through natal affiliation) the same area. Group-living can evolve when the (inclusive) fitness benefits of joining or remaining in a (natal) group outweigh the costs of sharing key resources (e.g. Alexander 1974; Emlen 1982; von Schantz 1984; Bacon et al. 1991; Koenig et al. 1992), and/or when there are strong ecological constraints on reproducing independently of the group (Lindström 1986; Hatchwell and Komdeur 2000; Kokko and Ekman 2002).

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Among many of the Carnivora, the benefits of group formation manifest through enhanced hunting ability, where packing power facilitates endurance hunting (e.g. grey wolves [*Canis lupus*], MacNulty et al. 2014), or strategic kills (e.g. lions [*Panthera leo*], Mosser and Packer 2009). There are, however, numerous group-living carnivores that do not hunt, or interact, cooperatively (see Kruuk 1975; Gittleman 1989; Creel and Macdonald 1995; Macdonald et al. 2004a; Macdonald and Johnson 2015; Noonan et al. 2015a).

In 1983, David Macdonald proposed the Resource Dispersion Hypothesis (RDH; see Macdonald and Newman, Chapter 6, this volume); that is, certain food (or other) resources can have dispersion and/or renewal rate characteristics that can permit several individuals to be accommodated within a single home range. Resultant 'spatial groups' need not necessarily have any cooperative basis, provided that cohabiting individuals can cope with the reduced food security that accompanies sharing resources. In this context, food security is a function of the diversity of food types consumed, the super-abundance of key food types at certain times, and the ability of the animal to binge during times of plenty and then store energy (as fat) as a reserve to sustain it during periods of food scarcity (e.g. drought, frost).

Competition is obviously most intense when food is scarce, testing the limits of group size—consequently torpor, or even hibernation, can alleviate pressure during less productive winter months. For a full review of the RDH see Macdonald and Johnson (2015).

Much of the work developing the RDH has been modelled using the European (formerly Eurasian) badger (*Meles meles*, overview in Macdonald et al. 2015b). For this facultative, but relatively uncooperative, group-living species, spatial groups can represent the most efficient and economic distribution of individuals under certain resource conditions.

Building on the RDH concept developed for *M. meles*, a sub-set of our author team compared the social system of *Meles* with that of the genus *Martes* (Newman et al. 2011). We concluded that, despite similar diet and taxonomic affiliation within the Mustelidae, martens are unable to achieve sufficient food security when sharing a territory. Because they must remain lean to hunt rodent prey effectively, martens cannot store sufficient fat reserves (unlike badgers) to endure times for shortage, and so cannot risk sharing their territory with conspecifics; unfed, a marten can starve within 72 hrs (Buskirk and Harlow 1989). This inability to store fat also constrains the ability of martens to engage in protracted torpor and precludes hibernation, unlike *M. meles*.

We have also established that the use of subterranean dens ('fossoriality') can promote continued (not necessarily cooperative) cohabitation at natal dens, as siblings mature into adulthood (Noonan et al. 2015a), provided that the habitat can meet the food requirements of this perpetuated group. Omnivory and dietary flexibility are thus important, enabling a wide variety of trophic resources to be utilized; strict predatory carnivores tend to disperse at maturity, unless benefiting from collaborative hunting. Ultimately, breeding groups of less related, or unrelated, individuals can arise through the exchange of dispersing individuals, often with promiscuous mating habits. The tendency for carnivores to be able to continue to co-occupy their natal den into adulthood is limited to those species weighing less than 15 kg, and so, functionally, group philopatry requires that species are big (fat) enough to tolerate periods of food deprivation, but not too big to share a den.

So, how should we test this trifecta, and elaborate on pioneering work on *M. meles*, where resources, fossoriality, and body-size all seem to facilitate group-living? By examining how these traits translate onto the societies of other taxonomically related and/or ecologically comparable badger species, of which the majority reside in Asia.

To paraphrase Whitcomb-Riley's (1848–1916) idiom, you might have thought that: '*If it looks like a badger, acts like a badger, and smells like a badger—then it's probably a badger!*'. Well, emphatically this is not the case; superficially similar badger species, or even the same species under different circumstances, can exhibit very different socio-ecology.

One trait that certainly does unify the badgers, and our working definition of their guild, is their ability to dig. Indeed, the common name 'badger' is derived from the French 'bêcheur', meaning 'digger', although sometimes also referred to as 'Brock' from the Proto-Celtic word 'brokko', for 'grey'. The proto-Indo-European root 'tek', meaning 'to construct', provides the origin of the name *Taxus*. Similarly, the Japanese, 'anakuma', means 'hole bear' (from 'ana' meaning hole and 'kuma' meaning bear), while the Chinese name for badger 'huan' means 'dog-like mammal'. Thus the consensus is that badgers are grey diggers, resembling small bears or dogs, which construct holes to live in; a broadly apt description.

But this is where the unity ends, because not all species that look and act like badgers are actually badgers. The African honey badger (or ratel, *Mellivora capensis*) and the Indonesian stink badgers (*Mydaus javanensis* and *M. marchei*, see Macdonald et al., Chapter 1, this volume) were formerly classified with the Melinae, due to eco-morphological similarities, but subsequently genetics has revealed them to be taxonomically different (see Koepfli et al., Chapter 2, this volume). As we shall see, even the taxonomic affiliation of the ferret badgers proves equivocal, but, in the spirit of a book about all musteloids, we include them in this chapter among the 13 extant species of true badger, in four genera, 11 of which have either all, or some, of their distribution in Asia. To these we add the more loosely affiliated honey badgers and stink badgers, also distributed in Asia, for completeness, as to not include something called 'a badger' living in 'Asia' might seem deficient to the uninitiated; although data on these species are sparse (Table 13.1).

Over the last decade, our team, assembled from China, Japan, and the UK, has pioneered investigation into these formerly little-known Asian badger species. We summarize our findings in this chapter according to two themes, the first being their socio-ecology. What can Asian badgers reveal about the paradigm of group-living? What are their social systems? How does habitat and resource availability relate to group formation? What roles do sett use, body-size, and torpor play in their ability to coexist? How do their social systems interact with mating systems? What are the implications of these socio-spatial geometries for territoriality? From this ecological backcloth we then proceed to consider conservation issues: how are the roles badgers play in ecosystem function impacted by the ever-present quintet of HIREC—Human-Induced

Table 13.1 Distribution, population trend, and conservation status of badgers

	Distribution				Population trend*	Conservation status*
	Asia	Europe	Africa	North America		
Genus *Arctonyx*						
Greater hog badger *Arctonyx collaris*	Y				Decreasing	Vulnerable
Northern hog badger *Arctonyx albogularis*	Y				Decreasing	Least Concern
Sumatran hog badger *Arctonyx hoevenii*	Y				Stable	Least Concern
Genus *Meles*						
European badger *Meles meles*		Y			Stable	Least Concern
Northeast Asian badger *Meles leucurus*	Y	Y			Unknown	Least Concern
Southwest Asian badger *Meles canescens*	Y	Y			Not evaluated	Not evaluated
Japanese badger *Meles anakuma*	Y				Decreasing	Least concern
Genus *Melogale*						
Bornean ferret badger *Melogale everetti*	Y				Decreasing	Endangered
Burmese ferret badger *Melogale personata*	Y				Unknown	Least Concern
Chinese ferret badger *Melogale moschata*	Y				Stable	Least concern
Javan ferret badger *Melogale orientalis*	Y				Unknown	Least Concern
Vietnam ferret badger *Melogale cucphuongensis*	Y				Unknown	Data deficient
Genus *Mellivora*						
Honey badger *Mellivora capensis*	Y		Y		Decreasing	Least concern
Genus *Taxidea*						
American badger *Taxidea taxus*				Y	Decreasing	Least concern
Genus *Mydaus*						
Sunda stink badger *Mydaus javanensis*	Y				Stable	Least concern
Palawan stink badger *Mydaus marchei*	Y				Stable	Least concern

*Evaluation by IUCN Red List (www.iucnredlist.org, Version 2016.3, accessed 7th February 2017)

Rapid Environmental Change (Sih 2013)? And, in light of ever-expanding human population pressure in Asia, what challenges face badger welfare and conservation in the region? Before we delve into these details, let us introduce the characters in our story.

Dramatis personae: Badger evolution, taxonomy, and distribution

The family Mustelidae has proven challenging for taxonomists and phylogeneticists (Koepfli et al. 2008a; Wolsan and Sato 2010; Sato et al. 2012; Koepfli et al., Chapter 2, this volume), owing to the diversity, and the relatively rapid rate of divergence, within their family tree (Bryant et al. 1993; Dragoo and Honeycutt 1997; Marmi et al. 2004). The precise taxonomic relationships within the Mustelidae are thus much debated (Sato et al. 2012; but see Koepfli et al., Chapter 2, this volume), and the badgers are no exception. Indeed, the species that was, until recently, referred to as the 'Eurasian badger' was originally mistakenly classified as a type of bear, *Ursus meles* ('honey bear'), by Linnaeus (*Systema Naturae*, 1758). Four years later, Brisson (1762) correctly re-assigned badgers to the Mustelidae.

Due to revolutions in nuclear and mitochondrial phylogenetics, the clan of badger species that formerly comprised the subfamily Melinae is now recognized as polyphyletic (Figure 13.1). Prior to this modern genetic revolution, however, taxonomic attribution was based on a series of anatomical features selected to reveal phylogenic associations (synapomorphies) rather than just ecological analogies (monoplasia): criteria still pertinent to fossil ancestors, devoid of useful DNA. Badgers were thus unified by basicranial anatomy and tympanic bullae construction (Qiu and Schmidt-Kittler 1982), loss of the supraorbital ramus of the medial meningeal artery (Flynn et al. 1988), and the loss of the suprameatal fossa. Their dentition united them via a broad posterior cingulum on premolar 4 (P^4), the enlargement of molar 1 (M^1) and of the talonid on M^1, with the concomitant reduction of the sectoral (cutting) region of the dentition—constituting an increased emphasis on grinding capacity (Ginsburg and Morales 2000; Kitchener et al., Chapter 3, this volume). In addition, badgers all share the canoid-type inflated bulla in which the hypotympanic sinus is inflated posterior to the promontorium; this latter feature is also found in their sister subfamily the Mustelinae.

The earliest recognized badger ancestor is *Melodon*, with skeletons recovered from China dating from the Upper Miocene to Lower Pliocene. *Melodon*'s dentition indicates a tendency toward increasing omnivory: shearing carnassials becoming reduced in proportion to an increasing emphasis on grinding, tubercular teeth (Kurtén 1968). It was also well equipped for digging, with a powerful body and long claws, and must have appeared very 'badger-like' in appearance.

Despite their name, Asian stink badgers are actually Old World skunks (see Macdonald et al., Chapter 1, this volume; Kopefli et al., Chapter 2, this volume), diverging from the rest of the mustelids at least 30 Mya (Dragoo and Honeycutt 1997). Nevertheless, many sources still classify them in the *Melinae*, and they blur the ecological distinction between badgers and the skunk subfamily (*Mephitinae*) (Figure 13.1). Radinsky (1973) first proposed that mephitines may be a sister-group to the *Melinae* and Wozencraft (1989) highlights the similarities in the auditory tympanic sinus and squamosal-mastoid region between the two taxonomic groups. The Indonesian stink badger, or teledu (*Mydaus javanensis*) and the Palawan, or Calamian, stink badger (*Mydaus marchei; Suillotaxus marchei* is an inferior subjective synonym), appear closely related. Both are endemic to Southeast Asia (Long and Killingley 1983) and, almost certainly, geographic isolation on the Palawan and Calamian Islands is responsible for their speciation.

The ferret badgers have also undergone recent taxonomic reappraisal, and are now generally classified into five species (see Macdonald et al., Chapter 1, this volume), including the newly recognized Vietnam ferret badger (*Melogale cucphuongensis*, Nadler et al. 2011), within their own subfamily, *Helictidinae* (Sato et al. 2004; Koepfli et al. 2008a; Wolsan and Sato 2010; Sato et al. 2012). These are curious affiliates of the badger clan, being rather small compared to other badgers (body-length 330–430 mm), but nimble predators, with more elongate bodies, long bushy tails, and sharp, pointed snouts. In many respects, therefore, they more resemble martens (genus *Martes*) (Newman et al. 2011). They are more primitive than any other living badger species, diverging from *Meles* and *Arctonyx* around 10–11 Mya (Koepfli et al. 2008a, Figure 13.1); evidenced anatomically by them having four premolars in each jaw, like the martens. They may well be behaviourally and morphologically similar to their early Miocene ancestors, such as *Melodon*, but intriguingly their remains have not been found in the fossil record prior to the Holocene (Simpson 1945).

With a wide distribution in Southeast Asia, hog badgers were, until recently, considered to include only one species, *Arctonyx collaris*, but recent evidence

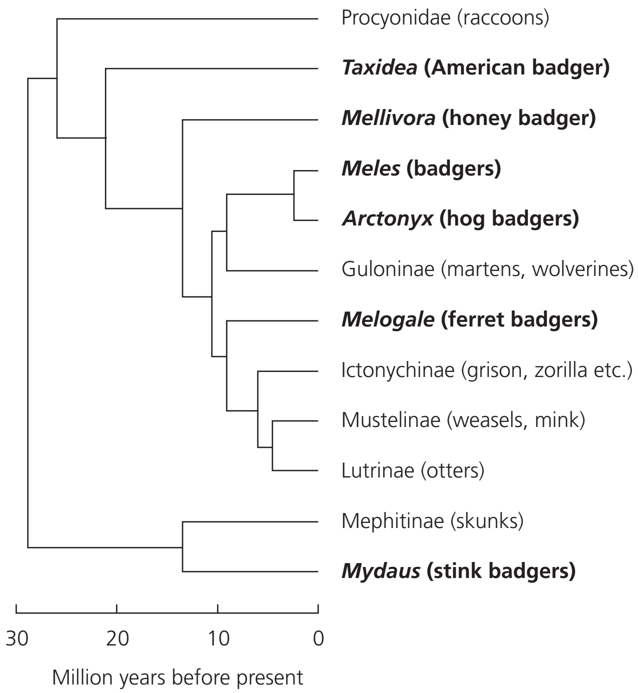

Figure 13.1 Phylogenetic relationships of badgers (bold) and related carnivores. Redrawn using data from Koepfli et al. (2008a) and Nadler et al. (2011).

indicates that there are in fact three species (Helgen et al. 2008a; see Macdonald et al., Chapter 1, this volume; Koepfli et al., Chapter 2, this volume). Notably, this means that our own work, cited in this chapter, pertains to the re-classified *A. albogularis,* whereas in our papers it was still known as *A. collaris* sub-species *albogularis* (L. Zhang et al. 2009; Chen et al. 2015; Y. Zhou et al. 2015a, 2015b). Similarity to *Meles* arises because *Arctonyx* and *Meles* both diverged from *Arctomeles* (Petter 1971; Ginsburg and Morales 2000) due to geographical isolation caused by the Himalayan orogeny.

The honey badger, or ratel (*Mellivora capensis*), is another meline imposter, which actually shares a closer ancestry with the stem Mustelinae (Vanderhaar and Hwang 2003); becoming sufficiently divergent about 12–13 Mya (Koepfli et al. 2008a) to warrant its own subfamily status in the Mellivorinae. This is mainly an African and Middle Eastern species, but has a distribution stretching into the Arabian and Indian peninsulas (Baryshnikov 2000; see Macdonald et al., Chapter 1, this volume).

The route that led the genera *Taxidea* and *Meles* to speciate had been unclear until recent work by Wolsan and Sotnikova (2013) demonstrated that *Ferinestrix* sp.—a distinctly larger and more carnivorous meline ancestor—originated in Asia and immigrated to North America, likely via the Beringian land bridge, no later than during the Pliocene. Notably, modern *Taxidea* have an auditory epitympanic sinus in the squamosal-mastoid region; a feature not found in the Old World *Melinae,* but present in the closely-related *Mephitinae* (skunks) (Wozencraft 1989). Koepfli et al. (2008a) argue that the American badger should be assigned to its own unique subfamily, Taxidiinae.

Even the most researched badger genus, *Meles*, was, until quite recently, comprised of just one species *Meles meles* (Kruuk 1989), divided into three regional subspecies. But again, morphometrics, combined with nuclear and mitochondrial phylogenies (Del Cerro et al. 2010; Abramov and Puzachenko 2013; Koepfli et al., Chapter 2, this volume) have distinguished four full species, which we adhere to in this chapter (see Macdonald et al., Chapter 1, this volume); although the fourth *Meles* sp., *M. canescens*, remains on the periphery of taxonomy and legislative acceptance.

Badger biology and socio-ecology

The societies of Asian badgers: exemplifying key traits underscoring group-living

While da Vinci taught us that simplification is the ultimate sophistication, badgers appear to contradict this dictum, because things are not simple and variation is manifest. As a starting position, let us reference the societal extremes book-ending the continuum of potential badger social geometries provided by the best-known badgers in the occident, *Taxidea taxus* (the American badger) and *M. meles* (the European badger). Powell's (1979a) description of the fundamental social geometry of carnivorous, predatory mustelids provides an accurate description of *T. taxus* (Goodrich and Buskirk 1998). *T. taxus* predate on prairie dogs or other colonial semi-fossorial rodents (Macdonald et al., Chapter 1, this volume; see also Weir et al., Chapter 19, this volume), which can be partitioned into one-animal helpings, where colonies can be monopolized. Consequently, carnivory results in discrete territories, prohibiting overlap except between the sexes during the breeding season.

In contrast, *M. meles* forms groups over many parts of its European range; although genetic analyses show that these are not nearly so exclusive or familial as once thought (see Macdonald et al. 2015b). Rather these are actually congregations of largely independent and minimally cooperative (*sensu* Eisenberg 1983) conspecifics (Macdonald et al. 2015b), drawn together by cohabitation in their communal burrow system (Noonan et al. 2015b; Ellwood et al. in press), termed a 'sett' (Thornton 1988). Thus, as Kruuk (1975) first highlighted, European badgers are among those species that live in groups without obvious benefits from integrated sociality; interacting little, not reliant upon allo-parental care (Fell et al. 2006; but see Dugdale et al. 2010), and travelling and hunting alone (Carr and Macdonald 1986).

Gittleman and Harvey (1982) stress how foraging ecology is central to understanding socio-spatial ecology and life histories, and Johnson et al. (2002b) showed this to be especially pertinent to regional *M. meles* population densities and social organization. *M. meles* group size varies enormously, and intraspecifically, across its European distribution, ranging from over 30 individuals in high-density, high carrying-capacity UK populations, down to breeding pairs in low-density, low-carrying capacity populations in parts of Continental Europe (Rodríguez et al. 1996; Brøseth et al. 1997; Remonti et al. 2006a; see Revilla and Palomares 2002). Lower densities and smaller groups are sustained mostly by fruits, cereals, and invertebrates, supplemented with small mammals and amphibians. Any tendency to form groups relates to the importance of earthworms in the badgers' diet, which are super-abundant and renew rapidly at the soil surface under favourable microclimatic conditions (Newman et al., Chapter 21, this volume); more worms leads to higher density and larger groups. Environmental conditions are also pertinent; food security varies more throughout the year in highly seasonal habitats than in more tropical ones. A sufficient food supply may cease completely during winter in cold climate zones; a circumstance some *M. meles* and *T. taxus* populations accommodate to varying extents through torpor or hibernation (Newman et al. 2011). *M. meles* are also highly olfactory, using scent to communicate individual-specific information (Buesching and Macdonald 2001; Tinnesand et al. 2015; Buesching and Stankowich, Chapter 5, this volume) and a conspicuous facet of their socio-spatial geometry is that they use their faeces to demarcate the interface between the periphery of each group's range (Buesching and Jordan, in press); although we add the caveat that at high density, in the UK, European badgers visit neighbouring groups regularly, with apparent impunity (Macdonald et al. 2008; Tinnesand et al. 2015; Ellwood et al. in press).

These behavioural and socio-spatial differences between well-known *T. taxus* and *M. meles*, combined with our emergent thesis on the basis to non-cooperative carnivore societies, leads us to a set of predictions that our research into Asian badger biology was conceived to test. We propose that any tendency toward group-living would be promoted, in degrees, by badger species:

1. eating a diverse diet of heterogeneously dispersed resources (especially earthworms)
2. large enough to cope with secondary food security under their conditions of daily and seasonal food availability (i.e. able to store body-fat), and able to reduce the effect of seasonal food constraints through torpor or hibernation
3. exhibiting extended natal philopatry/delayed dispersal—promoting the persistence of adult groups; a trait associated with the use of subterranean dens (termed 'setts', see Noonan et al. 2015b).

In opposition, any tendency toward discrete separate territories would be a feature of badger species constrained by being:

1. predatory/carnivorous—eating prey that can more easily be monopolized than shared
2. in less productive and/or more seasonal habitats (more reliant on hibernation)
3. among guilds of other competitor species (likely associated with highly productive and/or tropical areas of high biodiversity), where these interfere with food security for the badger species in focus.

We explore how these three promoters and three constraints fit Asian badger societies, recognizing that they may well have a hierarchical influence, with some precluding the effect of others. We also consider the implications of each species' social system for territorial organization and mating strategy, elaborating on whether traits established for European badger, such as delayed implantation (Thom et al. 2004b), superfecundation, superfoetation (Yamaguchi et al. 2006), and extra-group paternity (Dugdale et al. 2007; Annavi et al. 2014a,b), transcend the biology of other clan members.

The social organization of Asian badger species

The honey badger (*Mellivora capensis*)

Honey badgers eat pretty much any available animal prey (especially rodents, although aardwolf, bat-eared fox, and spring-hare are also eaten, along with birds, eggs, frogs, lizards, snakes, and insects—including scorpions; Kruuk and Mills, 1983), and like its North American cousin, they are almost exclusively carnivorous. This carnivory constraint (constraint 3) seems to trump any other factor that could promote group-living, because vertebrate prey tend not to have a dispersion that can be shared effectively (contravening our first promoter). As a consequence, honey badgers are fundamentally solitary (Begg et al. 2003a); where only mating partners have been observed hunting together (Rosevear 1974).

Notably, despite marked sexual size dimorphism, honey badgers do not exhibit intersexual differences in prey size preferences. Honey badgers tend not to have a distinct breeding season, followed by a 6–8 week gestation that, for a carnivore of this size, implies no substantial delayed implantation (Begg et al. 2005a). Their dens typically comprise a single tunnel 1–3m long, leading to a chamber, and they do not use bedding (Heptner and Sludskii 2002), even when females give birth to 1–2 cubs, which they rear alone. Exceeding the four months or so of maternal care seen in European badgers (Fell et al. 2006), honey badger cubs stay with their mothers for at least 14 months before becoming independent. Consequently, maternal–juvenile groups do persist, albeit temporarily (similar to *M. anakuma*, below), in accordance with our third promotor of group formation; although juveniles disperse when independent breeding territories become important. This long period of dependency is seemingly needed for cubs to learn how to hunt efficiently, which is crucial for honey badgers, occurring as they do in areas rich in intraguild hunting competitors; again militating against the food security necessary for group formation (constraint 3).

The Asian badgers (*Meles leucurus and M. canescens*)

Although systematic studies of Asian *Meles* spp. society are lacking, we can make inferences from their European cousins. They have a body-size congruent with the ability to form groups (promoter 2); however, they occupy continental interior habitats, characterized by aridity and harsh winters, potentially limiting their capacity to achieve food security under group-living scenarios (constraint 2).

As for the crucial influence of diet (promoter 1/ constraint 1), even within the taxonomically reformed European *M. meles* offshoot there is substantial intraspecific, facultative, regional food specialisms, adaptive to available food types (Revilla and Palomares 2002; Johnson et al. 2002a). To give us a baseline, *M. meles* is not restricted to an earthworm diet; for example it consumes predominantly rabbits in Doñana national park, Spain (Pigozzi 1991), and fruits in the Maremma national park, Italy (Martín et al. 1995)—and these trophic resources tend not to support group formation in these populations, lacking the dispersion characteristics to conform with promoter 1. *M. meles* diet also shows strong seasonal biases, such as switching to eat olives as they ripen in Portugal (Rosalino et al. 2005). Data on the diet of other *Meles* spp. are much more limited but, as described in Table 13.2, the feeding ecology of *M. leucurus* varies regionally, and dietary breadth seems broadly comparable to *M. meles* (Goszczyński et al. 2000; Li et al. 2013).

The southwest Asian badger (*M. canescens*) has only been recognized as a separate species since 2010 (Del Cerro et al. 2010; Abramov and Puzachenko 2013) and, to our knowledge, no systematic study has yet distinguished its feeding ecology distinct from *M. leucurus*. Surveying this species would be interesting because it has the most southerly distribution of the four *Meles* species, ranging over the Caucasus as well as the foothills of the Western Tien Shan Mountains in China and the Pamir-Alai Mountains in Russia. Arid foraging conditions are a limiting factor for the distribution of *M. meles* (Rodríguez and Delibes 1992) and these semi-arid and hot arid mountain biotopes likely restrict the diet and local distribution of *M. canescens*. In contrast, where *M. leucurus* is parapatric, it inhabits lowland semi-desert plains (Abramov and Puzachenko 2013).

Table 13.2 The diet of Asian badger species as described in the studies reviewed. Data are the relative frequency of each prey group.

	Locations	Coordinates	Sample size	Earthworm	Mammals	Birds	Reptiles	Amphibian	Fishes	Insects	Fruits	Molluscs	Others	Ref.
Genus *Arctonyx*														
A. albogularis	Southern China	29°48′N, 116°40′E	45	N/A	65.33	2.67	2.67	0	0	5.33	0	22.67	1.33	1
A. collaris	Northwest China	34°43′N, 106°42′E	57	27.32	2.19	1.09	0.00	1.64	0	38.80	26.78	1.09	1.09	2
A. hoevenii	Central China	30°5′N, 110°42′E	735	44.26	0.39	0.39	0.32	0	0	49.12	5.39	0	0.13	3
Genus *Meles*														
M. anakuma	Suburb of Tokyo, Japan	36°45′N,139°15′E	82	33.55	1.94	4.52	0	0.65		21.29	35.48	2.58	0	4
	Nagano, Japan		231	25.64	4.97	0.12	31.41	0	0	10.85	0.69	26.33	0	5
M. leucurus	Western Siberia			**	**	**	**	**		**	**		**	6
	Kazakhstan			**	**		**			**	**	**		7
	Southern Urals			72										8
	Middle Urals				**			**		**				9
	Mongolia	45°43′N,108°39′E	116	0	14.77	3.98	12.5	0		63.64	5.11	0	0	10
	Western Siberia	61°13′N, 69°4′E	204	18.14	7.93	3.78	0.25	4.79	1.76	27.71	35.64			11
M. canescens	North China	36°40′N, 100°48′E	162	0	3.34	5.41	13.54	0		68.45	8.87	0.4	0	12
M. moschata	Southern China		60	24.3	8.41	0	1.87	14.02	11.21	22.43	4.67	5.61	7.48	13
	Taiwan, China	24°46′N, 121°34′E	64	36.78	0	0	0	14.37	0	35.06	0	0.57	13.22	14
	Taiwan, China	24°04′N, 121°01′E	17	26.92	3.85	3.85	3.85	0	0	61.54	0	0	0	15

(*continued*)

Table 13.2 (Continued)

	Locations	Coordinates	Sample size	Earthworm	Mammals	Birds	Reptiles	Amphibian	Fishes	Insects	Fruits	Molluscs	Others	Ref.
	Central China	30°5′N, 110°42′E	163	N/A	5.12	1.86	0.93	0.47		66.51	25.12	0	0	16
M. everetti							N/A							
M. personata							N/A							
M. orientalis							N/A							
M. cucphuongensis							N/A							
Genus *Mellivora*														
M. capensis							N/A							
Genus *Mydaus*														
M. javanensis							N/A							
M. marchei	Palawan and Busuanga islands, Philippines	9°25′N, 118°29′E; 12°7′N, 120°10′E	N/A	N/A	N/A	N/A	N/A	N/A	N/A	**	N/A	**	N/A	17

**indicates that data are not available, and these food items are eaten by badgers. References: 1. Wang and Fuller 2003a; 2. Zheng et al. 1988; 3. Y. Zhou et al. 2015b; 4. Kaneko et al. 2006; 5. Yamamoto 1994; 6. Chashchin 2002, cited by Zagainova and Markov 2011, 7. Yanushevich and Blagoveshchenskii 1952, cited by Zagainova and Markov 2011; 8. Afanas'ev et al. 1982, cited by Zagainova and Markov 2011; 9. Zagainova 2009, cited by Zagainova and Markov 2011; 10. Murdoch and Buyandelger 2010; 11. Zagainova and Markov 2011; 12. Li et al. 2013; 13. Qian et al. 1976; 14. Chuang and Lee 1997; 15. Wu 1999; 16. Zhou et al. 2008b; 17. Kruuk 2000.

Table 13.3 shows how sett structure and use varies across different Asian *Meles* species, on both spatial and temporal scales. In some regions, *M. leucurus* uses large setts, similar to *M. meles*, extending up to 300 m^2, with up to 65 entrances; constructions clearly consistent with group-living (promoter 3). Reports from other regions describe group sizes ranging from 1 to 3, although these populations are sometimes subject to tremendous hunting pressure and habitat loss (Hao 2009; Li and Jiang 2014).

As with *M. meles, M. leucurus* has been reported to hibernate in setts, at least in colder and more arid parts of its range, that have unproductive winter seasons. In Mongolia, Murdoch and Buyandelger (2010) report inactivity from November through to April. This is an adaptation that can obviate extreme seasonal food restriction that could otherwise compromise group-living, if it occurs (mitigating constraint 2; although even solitary *Taxidea* hibernate in parts of their range, Weir et al., Chapter 19, this volume).

Like *M. meles, M. leucurus* mate from the end of March to the beginning of May in Northern China (Wang et al. 2015), and give birth a year later, around late March–early April, inferring that delayed implantation may be conserved across the genus. Unfortunately, data on *M. canescens* social systems, mating systems, and territorial organization are lacking. Based, however, on omnivory, trophic diversity, and regional populations consuming a significant proportion of earthworms (promoter 1), body-size (promoter 2), sett use (promoter 3), and hibernation (mitigating constraint 2), it seems plausible that they will fit into the continuum of group sizes observed for *M. meles,* and are thus likely to retain the same reproductive specializations seen among their congenerics.

As a counter-balancing force, extreme aridity and/or seasonal paucity in winter productivity (constraint 2), as well as intraguild competition (constraint 3; Murdoch et al. 2006), might limit food security in marginal areas. Consequently, group sizes may be highly habitat and/or region specific.

The Japanese badger (*Meles anakuma*)

A *Meles* species for which we have been actively working to elucidate socio-ecology is the Japanese badger (*M. anakuma*, Figure 13.2). Although a little smaller than its European cousins (4.2–9kg in the Hinode *M. anakuma* population compared with 7.5–10 kg in the Wytham Woods *M. meles* population, UK, Macdonald et al. 2015b; see also Macdonald et al., Chapter 1, this volume), the Japanese badger still seems large enough to tolerate periods of food scarcity by relying on body-fat reserves (according with promoter 2). Furthermore, Japanese badgers consume a significant proportion of worms in their diet: Yamamoto (1994) found that 96.1% of faeces (n = 231) included earthworms through the year, with a relative frequency of occurrence of 25.6% (Table 13.2). Given a diet potentially propitious to support group-living (in line with promoter 1), coauthor Yayoi Kaneko and colleagues undertook a more comprehensive study on *M. anakuma* diet in Hinode, near Tokyo, between 1992 and 1998 (Figure 13.3a). This area comprises a mosaic of different land uses such as woodland, grassland, paddy fields, farmland, irrigation ponds and canals, and small towns—termed a 'Satoyama' landscape in Japanese (Figure 13.3b). Here they found that *M. anakuma* exhibited wide dietary breadth and dietary switching (Kaneko et al. 2006). During spring and summer, earthworms (Megascolecidae spp.) occurred in 80% of 82 faecal samples

Table 13.3 Sett characteristics for three Asian badger species; data for other Asian species are not available in this detail.

Species	No. of setts	Sett density (setts/km²)	No. of badgers per sett	No. of entrances per sett	Entrance size			References
					Lengthwise	Crosswise	n	
Arctonyx albogularis	16	0.74	N/A	1.57 ± 0.76	26.36 ± 11.61	33.64 ± 16.17	27	L. Zhang et al. 2009
Meles leucurus	52	0.52	1.40 ± 0.70	N/A	N/A	N/A	N/A	Li and Jiang 2014
	43	5.57	N/A	4.27	N/A	N/A	N/A	Markov 2009
	6	N/A	2.17 ± 1.08	2.67 ± 1.70	N/A	N/A	N/A	Ye et al. 1999
	6	N/A	3.33 ± 2.75	23.33 ± 19.08	23.7	23.9	53	Hao 2009
	6	N/A	N/A	12.67 ± 2.49	25.75	32.11	76	H. Xu et al. 1997
Melogale moschata	14	0.65	N/A	3.36 ± 3.15	15.21 ± 4.66	16.64 ± 5.71	47	L. Zhang et al. 2009

Figure 13.2 A young adult male Japanese badger (*Meles anakuma*) trapped and immobilized during a population monitoring survey in Hinode, near Tokyo, Japan (2003). © Yayoi Kaneko

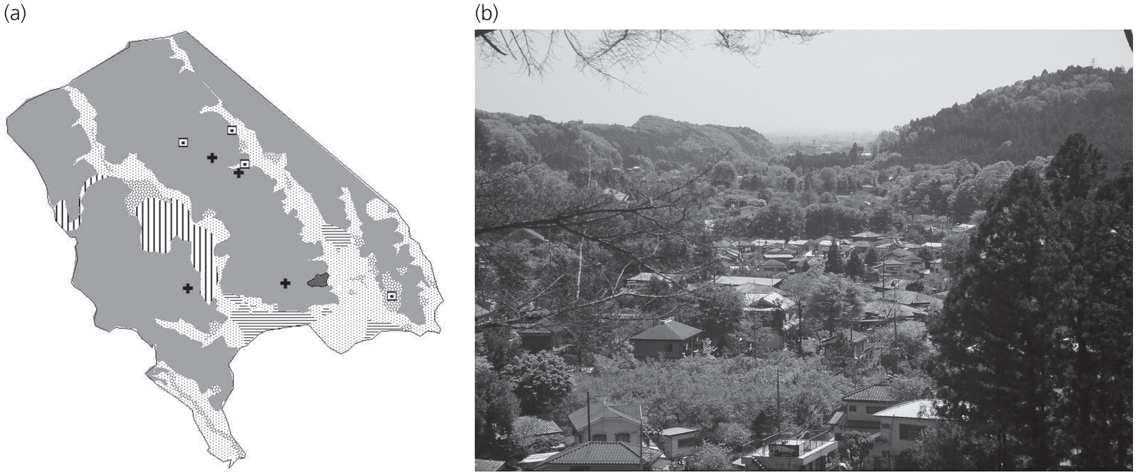

Figure 13.3 a) The Hinode landscape, showing the mosaic of different land uses comprising deciduous broadleaved forest (light grey), conifer plantation (dark grey), agricultural areas (dots), with industrial and dense residential areas (stripes)—a 'Satoyama' landscape. b) The study area in Hinode-town, near Tokyo, Japan (from Kaneko et al. 2006). © Yayoi Kaneko

analysed, supplemented with berries (30%) (*Rubus* spp.), beetles (35%), and persimmon (*Diospyros kaki*) (29%), and, crucially, badgers switched away from worms when persimmon became abundant in autumn. This dietary switching, often to consume not the most abundant food resource in the environment, but the most profitable one, arises when individuals seek to optimize the ratio of energy gained through foraging versus energy expended in food (especially mobile prey) acquisition (Charnov 1976a). Such optimal foraging is thematic across many of the generalist, omnivorous badger clan members (discussed in Y. Zhou et al. 2015b) as well as in other generalist mustelids; for example, our parallel work on the yellow-throated marten (*Martes flavigula)* in China (Zhou et al. 2011a). This suggests that the diet of *M. anakuma* may have the potential to support our first promoter of group-living (unfettered by constraint 1)—noting how the importance of earthworms influences *M. meles* group formation across Europe (Johnson et al. 2002b).

So what of Japanese badger society? Here, our own research, radio-tracking 21 individuals (14 males, 7 females) from our Hinode population (Kaneko et al. 2014), has exposed that more than just diet is at play.

Females with cubs had home ranges of consistently around 15.2 ± 6.3 ha throughout the year, and occupied small setts with 3.8 (± 3.1 SD; n = 12) holes. These home ranges were exclusive of other adult females and configured around areas rich in food resources, indicative of intrasex territoriality. We (Kaneko et al. 2014) posit that this 'obstinate strategy', under the Constant Territory Size Hypothesis (*sensu* von Schantz, 1984), likely serves to ensure a reliable supply of food resources (as determined by resource dispersion) for cub rearing. In contrast, males exhibited a flexible home-range strategy, expanding their exclusive home-ranges from an average of 33.0 ha (± 18.1 SD) in the non-mating season, to 62.6 ha (± 48.2) in the mating season, apparently to encompass the key resource of multiple oestrous females. This change in male interest in associating with females was reflected in the extent to which males visited latrines used by females during the mating season (see trace recorder system study by Kaneko et al. 2009b), potentially to learn her oestrous status and to reciprocate by leaving their own olfactory cues, in order to introduce themselves (see Buesching et al. 2016a). This sustained interest in females would also be promoted by superfoetation and superfecundation, extending polygynandrous mating opportunities through the summer, traits that *M. anakuma* seems likely to share with *M. meles*. Certainly, *M. anakuma* exhibits delayed implantation (Kaneko 2001) with post-partum mating occurring in April.

Male offspring shared a sett with their mother for up to 26 months, although the time actually spent with their mothers decreased steadily between 15 and 19 months old (similar to *Mellivora*). In contrast, female offspring remained with their mother for only 14 months, resulting in 1 of 5 instances of matriarchal territory inheritance. From microsatellite DNA analysis, we established that, across the population, mother and cubs comprised the basic social unit, supplemented by the retention of non-breeding juveniles or young adults, with males (less related to adult females than females were to each other) providing gene flow. This accords with our third promoter, that natal dens facilitate the formation of adult groups in the Carnivora, in suitable resource-scapes (Noonan et al. 2015b); although dispersal of juveniles at sexual maturity, to seek their own territories and mating opportunities, seems to be a critical threshold inhibiting stable adult group formation.

In addition, Japanese badgers also use their setts for winter torpor (Yamamoto 1997; Kaneko 2001; Tanaka 2006), and thus avoid the low-productivity limitations that might otherwise reduce the ability of offspring-maternal groups to persist through the first winter following birth (averting constraint 2). *M. anakuma* does, however, suffer intraguild competition from native raccoon dogs (*Nyctereutes procyonoides*) as well as introduced North American raccoon (*Procyon lotor*, see Threats, discussed further towards the end of this chapter)—making group formation susceptible to constraint 3.

Overall, the Japanese badgers' social system deviates from the basic musteloid pattern of solitary social spacing (Powell 1979a; see Macdonald et al., Chapter 6, this volume) and illustrates, within the genus *Meles*, a trajectory toward nascent group-living. Increasingly, we see that diet and resource dispersion (promoter 1) are foremost in underscoring badger congregation, enacted through the duration for which natal philopatry can be sustained. As Johnson et al (2002b) note for *M. meles*, the extent to which earthworms comprise diet relates to group sizes across Europe. Plausibly *M. anakuma* are on the cusp of vermivory being sufficiently important to sustain groups—explaining why females seek to monopolize territories exclusive of other females—but ultimately slip below the threshold where such a mechanism can allow offspring to stay within the mother's range as they themselves start to breed. This scenario mirrors the social system of *M. meles* in the southern and eastern parts of its European range.

The hog badgers (*Arctonyx albogularis*, with notes on *A. hoevenii* and *A. collaris*)

In contrast to well-studied Palaearctic *Meles* spp. the social system of hog badgers (*Arctonyx* spp., Figure 13.4) had, until our own recent work (Y. Zhou et al. 2015b), received only superficial investigation (e.g. Wang and Fuller 2003a; Zheng et al. 1988). *Arctonyx* spp. are broadly similar to *Meles* spp. in terms of body-sizes, cycles of seasonal weight change, and in using delayed implantation (possibly along with superfecundation and superfoetation) to extend the opportunity to achieve fertilization. Hog badgers might thus seem capable of group-living; able to maintain individual food security, in groups, in productive environments (according with promoter 2). Interestingly, this did not prove to be the case.

From our studies of the Northern hog badger, *A. albogularis* (formerly *A. collaris albogularis*) over three years in a subtropical forest of central China (Houhe National Nature Reserve, Hubei Province; 30° 5′ N,

Figure 13.4 Camera-trap photo of two northern hog badgers *Arctonyx albogularis* from the Houhe National Nature Reserve, Hubei Province, China. © Youbing Zhou

111° 42′ E, henceforth 'HNNR', Figure 13.5), camera-trapping (Y. Zhou, unpublished data) revealed that they appear to be solitary, despite eating a diet propitious for group formation (promoter 1). *A. albogularis* consumes a generalist diet, similar to *Meles*, but, as we described for *M. anakuma*, correlated with environmental food abundance only in part. Seasonal food Niche Breadth and Evenness indices both increased from the spring ($B = 1.94$, $J' = 0.64$) to summer ($B = 2.76$, $J' = 0.79$), indicative of opportunistic carnivory/insectivory (Y. Zhou et al. 2015b). Despite earthworms being abundant in the environment year-round in HNNR, and comprising almost 70% of total biomass consumed in spring, we saw dietary switching to a specialization on fruits when they were at peak environmental abundance in autumn, reducing these diversity indices to just $B = 1.14$ in autumn 2011 (close to 1 = specialization; and $J' = 0.20$) from 3.34 in that same summer ($J' = 0.77$) (Y. Zhou et al. 2015b).

Even though hog badgers are solitary in our HNNR study population, they still use latrines, but unlike European badgers in the UK, this is clearly not related to group territory defence (Y. Zhou et al. 2015a). Rather we found support for the 'foraging book-keeping hypothesis' (Henry 1977; Kruuk 1992; Remonti et al. 2011); that is, the intensity of latrine use exhibited a significant negative relationship with environmental food abundance, and was related to dietary output (faecal contents). The number of faeces per latrine reached seasonal maxima in early summer (4.2 faeces per latrine) but was lowest in autumn (0.7), and was significantly higher in logged and selectively logged forest, but lowest in farmland. Seasonal latrine use patterns thus signalled the importance of those resources most valued, in accord with 'Leontief's scarce factor paradox'; a concept in economic theory that states that the value of any commodity is function of its rarity (Valavanis-Vail 1954; Patterson 1998). In contrast, solitary *Mellivora* defecates throughout its territory (Begg et al. 2003b), and we infer *Taxidea* does similarly; although, surprisingly, this is not well established in the literature. We also found that Northern hog badgers dig setts with only 1.57 ± 0.76 (1–3) entrances (L. Zhang et al. 2009, Table 13.3); although whether this is causal or effectual in not forming groups due to extended philopatry (promoter 3) is impossible to say—nothing much is, as yet, known about offspring care.

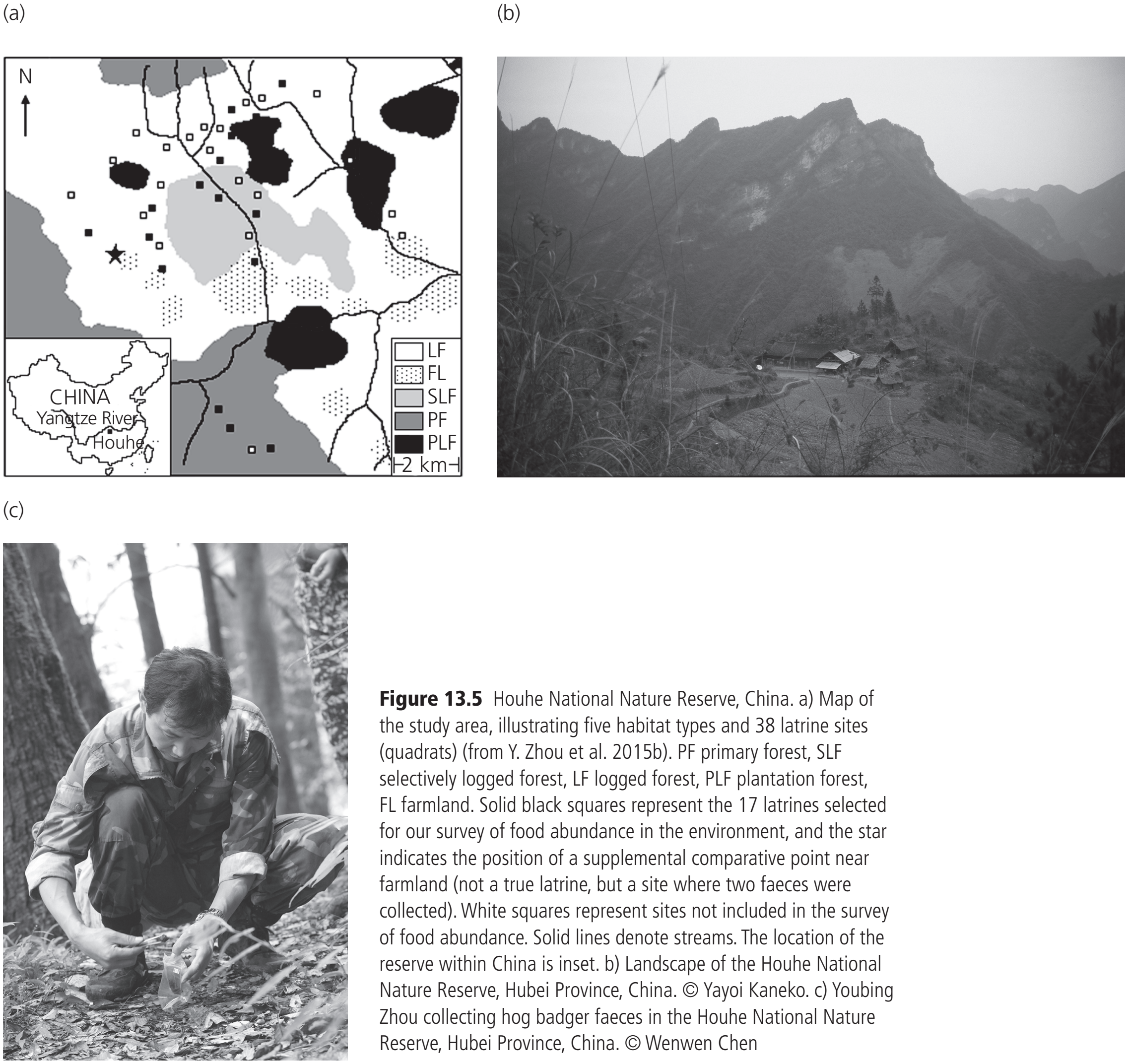

Figure 13.5 Houhe National Nature Reserve, China. a) Map of the study area, illustrating five habitat types and 38 latrine sites (quadrats) (from Y. Zhou et al. 2015b). PF primary forest, SLF selectively logged forest, LF logged forest, PLF plantation forest, FL farmland. Solid black squares represent the 17 latrines selected for our survey of food abundance in the environment, and the star indicates the position of a supplemental comparative point near farmland (not a true latrine, but a site where two faeces were collected). White squares represent sites not included in the survey of food abundance. Solid lines denote streams. The location of the reserve within China is inset. b) Landscape of the Houhe National Nature Reserve, Hubei Province, China. © Yayoi Kaneko. c) Youbing Zhou collecting hog badger faeces in the Houhe National Nature Reserve, Hubei Province, China. © Wenwen Chen

In comparison to *A. albogularis*, feeding ecology data for the more tropical Sumatran hog badger (*A.hoevenii*) and the greater hog badger (now known as *A. collaris*), remain deficient. By extension from our subtropical study (Y. Zhou et al. 2015b), we would predict that in tropical areas the availability of fruits year-round is likely to result in these being consistently the main dietary component, due their higher profitability (Y. Zhou et al. 2015b).

We see that hog badgers clearly satisfy the generalist, diverse omnivory of our primary promoter of group-living and so, given their size (promoter 2), their lack of group formation seems increasingly counter-intuitive. Furthermore, hog badgers have been reported to hibernate in their setts, at least in subtropical and temperate parts of their range, obviating constraint 2. For example, in our subtropical study area, they are inactive from December through to March (Zheng et al. 1988; Y. Zhou et al. 2015a, b), although in tropical zones hibernation might not be so prevalent. One possibility explaining their solitary social system may be that food security could be tipped below the threshold necessary for group-living due to competition from a substantial guild of trophic competitors, as per constraint 3 (Zhou et al. 2013a; see also Ross et al., Chapter 14, this volume).

The Chinese ferret badger (*Melogale moschata*)

Also in HNNR, our own work, radio-tracking nine (six males, three females) of 22 Chinese ferret badgers (see opening photo) caught, has revealed that these individuals were affiliated into three groups. The largest of these groups comprised at least seven tracked individuals with overlapping ranges, including at least four adults, which cohabited within the same sett. This is the first confirmation of group-living and sett sharing for badgers outside of the genus *Meles*, and group sizes are minima, because un-tracked ferret badgers will also be affiliated to these groups. Consistent with group-living, our camera-trapping data further revealed that ferret badgers deposited their faeces in latrines (Zhou et al. 2008b) shared by the other individuals co-utilizing the same area (Y. C. Wang, personal communication; Y. Zhou et al., unpublished data).

Mean (± SD) 100% minimum convex polygon home range size was 128.3 ± 131.9 ha, with no difference between sexes. Movement distances and activity per diem patterns also did not differ between the sexes. Seasonal activity rates were lowest in December (33.1%) and increased gradually through the spring and summer to peak in June (52.6%). Chinese ferret badgers mate from February to April and gestation appears to last variably for 60–80 days; longer than the typical physiological requirement of around 50–60 days for a carnivore of this size (Pei and Wang 1995; Li 1996; Wang and Fuller 2003b). This suggests that there may be a short delay to implantation, as seen in other mustelids, such as American mink (*Neovison vison*, Macdonald et al. 2015a).

We also collected 163 faecal samples through autumn and winter 2004–2006 for dietary analysis (Zhou et al. 2008b), and found that *M. moschata* ate principally insects and fruits in HNNR; notably, fleshy-fruited and seed-pulp rich species. This diet satisfies our first promoter, congruent with our observation of group-living. Nevertheless, studies of ferret badgers in southern China (60 stomach contents) (Qian et al. 1976) and Taiwan (16 stomach and 60 faecal samples) (Chuang and Lee 1997; Wu 1999) report diets comprised largely of earthworms, arthropods (insects), and amphibians (frogs). This could indicate that there may be intrageneric, and even intraspecific, variation in ferret badger socio-spatial systems, relating to local dietary choices and resource dispersion.

Although ferret badgers consume food resources favouring group formation (promoter 1), their society otherwise strains our thesis. We would have anticipated that small body-size (at 1–3 kg; morphologically resembling solitary martens) might have constrained them to a solitary lifestyle; that is, they seem to contravene promoter 2 (Newman et al. 2011). And even though activity was reduced in winter, there was no evidence of sustained inactivity or torpor for any individual tracked, which indicates that ferret badgers do not hibernate (Zhang et al. 2010)—exposing them to the risks of insufficient food security during winter (constraint 2, militating against group-living). Plausibly, however, given that ferret badgers do not need to maintain the predatory and arboreal agility characterizing martens, they may well be able to combine small body-size with an ability to carry fat. That is, they will meet their per capita resource security needs more easily than do sympatric, solitary, but larger *Arctonyx*, where the RDH predicts that group size is a function of food patch richness (see Macdonald and Johnson 2015). Smaller size and/or lower energy needs may also make ferret badgers more competitive (compared with hog badgers) among the guild of small carnivores they are sympatric with (see Ross et al., Chapter 14, this volume).

Chinese ferret badger setts are also small, with 3.36 ± 3.15 (range 1–12) entrances (L. Zhang et al. 2009; Table 13.3), although, because this species is physically smaller than other badgers, their burrow systems still clearly allow congregation. Camera trapping indicates that juveniles accompany their mother (i.e. an adult female) when foraging, implying that natal philopatry (prediction 3) might play a role in perpetuating social group formation in this species (Noonan et al. 2015b). To our knowledge, no systematic studies have yet been conducted on other members of the *Melogale* genus.

The stink badgers (*Mydaus* spp.)

Although information on stink badgers is fundamentally lacking, no systematic observers (such as Grimwood 1976; Kruuk 2000) report congregation or sett cohabitation for *M. marchei* or *M. javanensis*. Instead, they occupy short, simple burrows, in which two to three young are raised by only their mother (Long and Killingley 1983). Nothing substantial is reported about their mating systems (e.g. Hwang and Larivière 2003), although taxonomically one might look for similarities to polygynous New World skunks, that do not exhibit delayed implantation, rather than Old World badgers.

This lack of group formation is puzzling because observations of stink badger foraging behaviour indicates broad omnivory, with diets similar to skunks; conditions generally facilitating group-living (promoter 1). Hwang and Larivière (2003) report that Sunda stink badgers (*Mydaus javanensis*) eat mostly invertebrates, eggs, and carrion, and the diet of the Palawan stink badger (*M. marchei*) can include freshwater crabs, as well as small insects, which they dig up using their long claws (Kruuk 2000). And while stink badgers are small (1–2 kg, discordant with the tenets of promoter 2), they are a similar size to group-living ferret badgers occurring in similar tropical forest. Whether stink badgers use latrines, and, if so, how, remains a mystery, although given that true badgers often do, and that new world skunks also do, it seems likely that more remains to be discovered about latrine use and territory patterns in *Mydaus*.

Phylogenetically, group-living is not a prevalent feature of New World skunk society. Only natal groups, and co-occupation of over-wintering dens by multiple females, or multiple females and a single male, are recorded for the striped skunk (*Mephitis mephitis*, Wade-Smith and Verts 1982; see also Hass and Dragoo, Chapter 24, this volume). So, although it is an unsatisfying explanation, perhaps there is inertia against group formation in this taxon.

Ecosystem function of badgers, threats, and conservation priorities

While Asian badgers have allowed us insight into the suite of factors relating to group-living in societies that do not arise primarily through benefits of collaboration, they are not merely interesting for their own sake. They also perform important ecosystem functions in tropical forests—roles that are impinged upon by HIREC factors (Sih 2013), especially habitat loss and climate change. What's more, like European badgers, they are variously threatened by direct human-wildlife conflicts, as well as intentional persecution.

Taxonomic revisions that jeopardize wildlife law enforcement

There have been substantial revisions to badger taxonomy over the last decade, and, as we have described, the assignment of certain Asian badger species to distinct subfamilies (e.g. Helictidinae), or even whether certain species are recognized as unique or not (e.g. *M. canescens*), remains equivocal. These confusing taxonomic revisions are more than just an irritation for ecologists and conservationists, they have real implications for the protected status of badgers, as well as many other species.

The Shakespearean soliloquy of 'What's in a name?' (Romeo and Juliet, Act II, Scene II) has a worrying pertinence in China, where our team has revealed (Z. Zhou et al. 2015a, 2016) that if a species changes its binomial name (in accord with taxonomic revisions) this may result in it no longer being identifiable on China's Protected Species List (PSL; see State Council 1988, www.forestry.gov.cn). This list has not been updated since it was enacted in domestic Chinese law in 1989, and consequently various species are, increasingly, becoming known by different synonymous binomials between China's PSL and CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora). This hinders the compilation of accurate data on illegal wildlife trade, and creates judicial and political ambiguity. Furthermore, when species that were once designated as exotic (e.g. pangolins), and thus prosecutable under CITES, become recognized as having an endemic distribution, they can no longer be proven beyond reasonable doubt to have been imported (i.e. international trade), and thus sentences applicable for illegal exploitation and trafficking can only be sought under the PSL, which is far more lenient, no longer including life imprisonment. Certainly, although these 'new' species of badger, emerging since 1989, are recognized by the International Commission on Zoological Nomenclature (iczn.org), and by China's 'Scientific checklist of China's Mammal Species' (Jiang et al. 2015), they are not included in Chinese legislation. As more badger species become imperiled and thus listed by CITES, this will need to be resolved, else criminal traders in China will use this loophole to evade prosecution, as is already the case for other mis-listed species.

The effect of extreme weather or roles in seed dispersal and forest recruitment

Due to their consumption of fruits, nuts, and seeds, badgers can play an important role in both endozoochorous (seed ingested and defecated) and epizoochorous (external seed carrying) seed dispersal (Pigozzi 1992; Rosalino and Santos-Reis 2009; Rosalino et al. 2010; Gallagher 2014), with important implications for ecosystem functionality and forest regeneration (Howe and Smallwood 1982; Bascompte et al. 2006; Gallagher 2014).

Our research in HNNR (Zhou et al. 2008b, 2013b, 2013c) found that Chinese ferret badgers are legitimate (they defecated viable seeds), but inefficient, seed dispersers (seeds in faeces were deposited mainly in the open at 'unsafe microsites' for seed germination and seedling establishment), although they may be effective at transporting seeds between forest stands in fragmented habitats (Zhou et al. 2008b). We also found that the Northern hog badger may play a significant role in endozoochorous seed dispersal process (Y. Zhou et al. 2015b), because of its preference for fruit during the autumnal peak in fruit abundance (consuming fruit from at least 10 plant species, RFO 65%). In particular, we discovered that these badgers, along with a guild of small carnivores, are critically important as endozoochorous seed dispersers for a dry-fruited plant, the raisin tree (*Hovenia dulcis*, Zhou et al. 2013c). The raisin tree bears nutritious, enlarged, twisted brown peduncles to entice consumption of the external black seeds that these carry.

In terms of ecosystem functionality, we were the first to establish how this obligate seed dispersal mutualism is vulnerable to climatic perturbations (e.g. extreme weather events, Zhou et al. 2013b). For example, it is not expected to snow in subtropical China, nor are temperatures expected to dip below freezing for extended periods, even at high elevations. In January–February 2008, however, an extreme frigid period coincided with our dietary studies, which reduced seed dispersal function for many trees substantially; the raisin tree lost 96% of its seed dispersal in this 2008 fruiting season, compared to the mean of the previous two years. It was not that trees did not fruit—they did—but that the entire guild of omnivorous carnivores in the forest shifted from fruit consumption to eating predominantly small mammals and birds—probably due to a greater need for protein under cold conditions (King and Murphy 1985). Degraded forest areas were particularly susceptible to these effects. While European badgers are vulnerable to weather variability (Newman et al., Chapter 21, this volume), we see that extreme weather conditions can also disrupt the foraging ecology, and thus ecosystem role, of hog and ferret badgers.

Habitat loss due to urbanization and forest loss

Worldwide, habitat loss causes higher local extinction rates, and endangers more species, than any other conservation threat (Brooks et al. 2002). Because Asian badgers eat diverse diets, relying upon mixed food types, and also because they tend to conceal their setts in dense vegetation (L. Zhang et al. 2009), they have specific habitat requirements, sensitive to forest thinning and cutting.

Urbanization is a major cause of habitat destruction (McKinney 2002), and urban development is of serious environmental concern across Asia (Fang 2009). The European badger can cope with only moderate levels of urban development (Davison et al. 2009); however, the Japanese badger seems particularly adept at tolerating human encroachment (Kaneko et al. 2006, 2014). In the Greater Tokyo metropolitan area, Japanese badgers are expanding into more urban districts. Working with Dr. Kamito, co-author Yayoi Kaneko (unpublished data) has records of 26 setts over 62 ha in Mitaka-city, a suburb 20 km from central Tokyo. Moreover, in Kaneko's Hinode-town study area, 50 km from central Tokyo, badgers rely heavily on food provided by local people in their gardens.

Other badger species prove more vulnerable to extirpation. A survey in suburban Shanghai in 2007 (Hao 2009) found that, where *M. leucurus* had formerly been numerous prior to urbanization, only 28 individuals remained, living in seven isolated setts spread over 6341 km^2. Worse, by 2009, three of these seven setts had been enveloped by urban sprawl (Li et al. 2010). Even in HNNR, half of all badger setts (n = 30) studied suffered from some extent of human disturbance, with one sett heavily disturbed (L. Zhang et al. 2009).

Setts are an important resource (Noonan et al. 2015a), and in the subtropical forests of central China, hog badgers sometimes share setts with ferret badgers (Zhou et al. unpublished data; L. Zhang et al. 2009). Badgers even risk being usurped by rival species. In Japan, intraguild competition for setts can be an issue for Japanese badgers competing against native raccoon dogs (*Nyctereutes procyonoides*) and worse, larger and more aggressive introduced North American raccoons (*Procyon lotor*), that displace badgers (Ikeda et al. 2004; Matsuo et al. 2007).

Although honey badgers are strong diggers, and usually excavate their own dens, they occasionally exploit disused warthog burrows, or aardvark holes dug into old termite mounds (Rosevear 1974). Similarly, stink badgers are often commensal on dens dug by porcupines (Hwang and Larivière 2003).

The effects of road development

Another problematic component of urbanization is that unwary badgers are often involved in road-traffic accidents (RTAs, see Macdonald et al. 2010b), and badger populations thus suffer from the habitat fragmentation roads cause (Forman et al. 2012). RTAs are a substantial problem for *M. meles* across Europe (Davies et al. 1987; Aaris-Sørensen 1995) and RTAs are clearly a substantial mortality factor for badgers in Japan (Saeki and Macdonald 2004) and across Continental Asia (Wang et al. 2013).

An opportunity arose for us to study this issue when a network of roads and pathways was developed in HNNR to facilitate burgeoning ecotourism (Zhou et al. 2013a). Higher trail use along more major trail types was associated with significantly fewer small mammal (e.g. rodent) field-signs along transects close to these trails, compared with more distant transects. In contrast, hog badger and ferret badger field-signs were unaffected by proximity to roads (Y. Zhou et al. 2013a). Indeed, badgers likely profit from roads by utilizing the easy opportunity roads provide to commute across territory. Traffic is, however, more problematic. In HNNR, co-author Youbing Zhou observed two hog badger and five ferret badger RTAs during a visit in spring and summer 2006. Similarly, Zhou noted three ferret badgers run over during fieldwork in Shennongjia Reserve in the summer of 2010.

Hunting badgers for food and as a source of medicinal products

Although the impacts of the legal and illegal wildlife trade are broadly recognized for flagship species in Asia (e.g. elephant, rhino, tiger, pangolin), we have been taking a lead in highlighting the exploitation of more common and less charismatic species, which has, thus far, not received the attention it warrants (Z. Zhou et al. 2014a, 2014b, 2015b, see also Harrington et al., Chapter 7, this volume for a review of exploitation of the musteloids) compounded by legal deficiencies permitting this exploitation (Z. Zhou et al. 2015a, c, 2016). Of special concern is that demands for wild game species, and derived products, are actually increasing in China (Z. Zhou et al. 2014b, 2015a, 2015c).

As with European badgers, badgers have been hunted for millennia across Asia to provide meat, leather, pelts, but also bristles used for shaving brushes (Domingo-Roura et al. 2006) and fat, used for cooking, waterproofing clothes, and even to manufacture soap (Chen and Liu 2000). Significantly, badgers also have a role in the Asian traditional medicinal pharmacopaeia, with products applied to treat burns, scalds, gastric ulcers, and even haemorrhoids (Li 1982). Co-author Yayoi Kaneko has visited ‘badger farms’ in South Korea, stocked mostly by *M. leucurus*. There badgers are listed as livestock, and badger derivatives are popular treatments for burns, atopic dermatitis, and stomach cramps. They are also used to make skin lotion and bile liquor; an alternative to black bear bile liquor (see Dutton et al. 2011). Of concern too is that these farmed badgers, often of foreign origin, frequently undermine fences and escape into the wild, with ecosystem and wildlife disease implications.

The Japanese badger remains a popular game species, although numbers hunted in Japan—mostly for sport—declined from 7000 individuals per year in the 1970s to less than 2000 in the late 1980s, and to 1050 in the Japanese Ministry of the Environment report for 2012 (www.env.gov.jp). Kaneko et al. (2009) proposed this reduction was more likely due to a loss of interest in hunting generally rather than intrinsic wild population declines. Noteworthy too is that, unlike the tradition in Europe of flushing badgers from setts with terriers (now illegal in UK), the practice in Japan (and the only legally approved method of sport-hunting in Japan today) is to dig badgers out of their sett during their winter torpor.

The hunting of badgers, to provide food as ‘bushmeat’, is still quite prevalent in parts of Continental Asia (Figure 13.6); Lee et al. (2004) reported that up to 620 hog badgers and 520 ferret badgers were sold each day in markets in Guangzhou and Shenzhen (China), with smaller numbers of wild-caught *M. leucurus* for sale in wildlife markets in Guangdong and Guangxi cities (Ades 1992; Lee et al. 2004). Lau et al. (2010) warn that, due to intense illegal hunting and trapping for food in southern China, hog badger populations appear to be in rapid decline, risking regional extirpation.

This concern prompted us to investigate the effect of hunting on the genetic diversity of a hog badger population in Hubei Province, China (Chen et al. 2015). We collected DNA samples from hog badgers, confiscated from illegal traffickers and local hunters by forest authorities, in the market towns of Wufeng and Yuguan. Using novel hog badger genetic microsatellite markers that we developed, we found that, despite 40 km separation between towns, seized hog badgers exhibited no genetic evidence of spatial segregation. Mean alleles per locus were 8.33 and genetic diversity was high: mean expected heterozygosity [H_E] was 0.77, consistent with that reported for European badgers sampled over extensive regions of continental Western Europe ($H_E = 0.70$, Pope et al. 2006). Our findings implied that these confiscated hog badgers belonged to the same meta-population and that the social structure of the regional population had been eroded by hunting. From this we concluded that the exploitation of this wild source population was causing significant impacts on natural population dynamics.

Figure 13.6 a) A hunted Asian badger (*Meles leucurus*) and b) an Asian badger (*Meles leucurus*) prepared for bushmeat, at a market in Zhong county, Chongqing Municipality, China. © Youbing Zhou

A final word on this topic, eating badgers can make you sick: Lee et al. (1999) report from South Korea that badgers are often infected with the nematode *Trichinella spiralis*, and thus consuming contaminated liver and blood can cause fever, myalgia, periorbital oedema, and eosinophilia.

Human-badger conflict: deliberate persecution/management

Aside from the issues of urbanization and hunting for food and medicine, badgers can come into direct conflict with other human enterprises, particularly farming (Baker and Macdonald 2015; see also Harrington et al., Chapter 7, this volume). In China, badgers are particularly attracted to maize, potato, and sweet potato crops. In Japan they can be a pest for the production of ground-fruits, such as strawberries and watermelons. Aside from direct damage, they can unearth crops and damage flowers when they dig for earthworms and invertebrates, especially soil-dwelling insects such as the larvae of crane flies (Tipulidae) and chafers (Scarabaeidae). Badgers also occasionally predate on farmed chickens and are even accused of taking lambs, and cause a general nuisance in rural Asian villages. These problems often lead to retaliatory killing, with co-author Youbing Zhou coming across examples of farmers snaring and/or poisoning badgers on their farmland in China. In the low-density population of *M. leucurus* around suburban Shanghai, two of the 28 badgers recorded there were snared by a local farmer to protect watermelons against damage (Hao 2009). We have recently uncovered startling new data from Japan, showing that farmers in some areas have suddenly taken to killing badgers by the thousands, to protect against alleged crop damage (Kaneko et al. 2017). Culling methods are often cruel and the pressure on regional populations seems unsustainable.

Badger excavations also occasionally undermine agricultural buildings, roads etc. (see Harrington et al., Chapter 7, this volume), and disrupt irrigation. In Japan, 4595 badgers were killed by government decree in 2012, although many of these were connected to the raccoon eradication programme in Japan, dying in leg-hold traps, especially on Kyushu island (an unintended outcome that Yayoi Kaneko is currently investigating). A particularly serious problem arises when badgers dig through river flood-defences and/or levees, which has occurred on the Yellow River (Zhang 1982) and Qiangtang River (Zhu 1998). This extremely dangerous issue is dealt with by digging badgers out of their setts and killing them (Zhang 1982; Cai 1993).

Zoonotic disease control

European badgers are well established as wildlife hosts for bovine tuberculosis in the UK (Woodroffe and Donnelly, Chapter 20, this volume; see also Macdonald et al. 2015b) and musteloids generally are susceptible to a variety of diseases (Newman and Byrne, Chapter 9, this volume). Undoubtedly, the disease pairing of greatest concern for Asian badgers is rabies in ferret badgers (S. Zhang et al. 2009; L. Wang et al. 2014). H. Wu et al. (2014) reports an outbreak of rabies in Taiwan in which 31% of 512 ferret badgers tested positive.

The mortality arising through rabies epizootics is not a major threat to the viability of ferret badger populations, but rabies poses a significant threat to human health (L. Wang et al. 2014), and is perceived with great fear in China (Yin et al. 2013). In response to outbreaks, the Chinese government's policy is to cull, snare, and poison badgers (and other meso-carnivores) in the region affected (Gong et al. 2012). The honey badger is also a minor vector of rabies within its range (Röttcher and Sawchuk 1978), while in Indonesia, Sunda stink badgers are implicated in rabies outbreaks (Joseph et al. 1978), and new world skunks act as a major pool of infection in North America (Newman and Byrne, Chapter 9, this volume).

Ferret badgers, along with masked palm civets (*Paguma larvata*), were originally also implicated as a zoonotic vector of Severe Acute Respiratory Syndrome Coronavirus (SARSCoV—Guan et al. 2003) in China—although this subsequently proved incorrect; the true hosts are bats (W. Li et al. 2005). Initially, however, government policy was to cull ferret badgers and civets; notably, hog badgers were never implicated directly in SARS transmission.

Significantly, a change in attitude among the general public in China, led by debate in the media, is gradually resulting in reluctance to accept the widespread destruction of wildlife for any purpose, including to control disease. In the longer term, vaccination is being explored as an alternative strategy to deal with zoonotic disease epidemics (Haydon et al. 2006).

Synthesis: the same, but different

- *Meles* spp. all seem superficially similar, but can behave quite differently, and have different social systems, both intra- and interspecifically, depending on regional diet resource conditions.
- Hog badgers (*Arctonyx* spp.) are eco-morphologically similar to *Meles*, and appear to eat a similarly versatile and omnivorous diet over much of their range, and yet they do not form groups.
- Chinese ferret badgers (*Melogate moschata*) look quite different to these other badger species, being smaller and more marten-like, and yet they exhibit group-living comparable to certain *Meles* spp. populations, notably to *M. anakuma*; certainly their lifestyle is quite different to the martens they resemble (other *Melogale* spp. remain data deficient).
- The honey badger (*Mellivora capensis)* behaves in a very similar way to the American badger (*Taxidea taxus*), occupying a similar ecological niche and being solitary—and yet taxonomically, it is not a badger at all, just a convergent mustelid.
- Stink badgers (*Mydaus* spp.), which look like badgers but are, phylogenetically, skunks, are solitary, despite eating a similar diet to ferret badgers in similar tropical habitat.

While this variability is extraordinary, for such a superficially similar clan, there are nevertheless themes (summarized in Table 13.4). Foremost, badgers (and pseudo-badgers; e.g. *Taxidea* and *Mellivora*) that are strictly predatory/carnivorous (constraint 1) never form persistent adult groups. In contrast, the consumption of a diverse, omnivorous diet (promoter 1) enhances the likelihood of group-living and delayed dispersal (promoter 3). These trophic factors seem incontrovertible across the badger guild, and beyond, among other non-collaborative group-living carnivores—unless these key precursors are suitable, group-living tends not to evolve. Natal philopatry is additive to this diet-/resource dispersion-based mechanism propitious for group-living (Noonan et al. 2015b). The RDH describes how secondary individuals might be accommodated within the territory of the primary pair, provided they can accept the consequential reduction in secondary food security this entails (see Macdonald and Johnson 2015). Where might these secondary individuals arise from? Although they could be adults accreted into the group, inevitably primary pairs produce offspring, and we see among badger species the variable extent to which offspring remain philopatric, or disperse. In both *M. anakuma* and *Mellivora*, juveniles remain with their mother for around one and a half years (i.e. beyond the time she produces her next litter). Only then, as resources get tight, and maturing juveniles seek their own breeding territories, do they disperse. In carnivorous *Mellivora*, dispersal seems inevitable, but among other *Meles* spp., especially those eating mostly earthworms, conditions of trophic productivity and dispersion often allow group-living to perpetuate into adulthood, where *M. anakuma* seems to

Table 13.4 Summary of how predictors of group formation (promoters and constraints) apply to Asian badger species. DD = data deficient.

	Predictors of group-living			Constraints on group-living			Noting regional / intraspecific variation
	1	2	3	1	2	3	
	Omnivory / diverse diet	Large enough to withstand secondary food security, but <15kg	Using sett / delayed dispersal / philopatry	Predatory carnivory	Seasonal food paucity (mitigated by torpor)	Intraguild competition for resources	Capable of group-living?
Arctonyx collaris	Y	Y	Y/?/?	N	Y(Y)	Y	N
Arctonyx hoevenii	Y	Y	(DD)	N	(DD)	Y	(DD) – unlikely
Arctonyx albogularis	Y	Y	(DD)	N	(DD)	Y	(DD) – unlikely
Meles meles	Y	Y	Y/Y/Y	N	Y (Y)	N	Y
Meles leucurus	Y	Y	Y/?/Y	N	Y (Y)	Regionally	Y?
Meles canescens	Y	Y	Y/?/?	N	Y (Y)	Regionally	Y?
Meles anakuma	Y	Y	Y/Y/Y	N	Y (Y)	Y	Maternal-offspring with delayed dispersal
Melogale moschata	Y	Rather small?	Y/Y/Y	N	Y/N (reduced winter activity)	Y	Y
Melogale personata	Y	Rather small?	(DD)	N	N (DD)	Y	(DD)
Melogale cucphuongensis	Y	Rather small?	(DD)	N	N (DD)	Y	(DD)
Melogale orientalis	Y	Rather small?	(DD)	N	N (DD)	Y	(DD)
Melogale everetti	Y	Rather small?	(DD)	N	N (DD)	Y	(DD)
Taxidea taxus	N	Y	Y/N/N	Y	Y(Y)	N	N
Mellivora capensis	N	Y	Small/Y/N	Y	N	Y	N
Mydaus javanensis	Y	Rather small?	Small den/N/N	N	N (Probable)	Y	N
Mydaus marchei	Y	Rather small?	Small den/N/N	N	N (Probable)	Y	N

fall just onto the cusp of Johnson et al.'s (2002b) extent of vermivory facilitating sustained groups.

Secondarily to the role of diet, and the interactive role of philopatry, the ability to store body-fat (promoter 2) also proved important. That ferret badgers can attain sufficient individual food security to live in groups, despite being only a little larger than solitary martens was counter to our prediction here. We stress the caveat, that, so far, only our study has observed group-living in ferret badgers, and that their diet at our site aligned with promoter 1, favouring group-living. Ferret badger diet appears to differ extensively among populations, suggesting intrageneric and intraspecific variation in social systems. Certainly, they do not need the lithe athleticism to hunt and climb that typifies *Martes*, and so can be more rotund, and their (sub)tropical distribution reduces the extent to which productivity becomes a constraint in winter. Furthermore, we speculate that, being smaller (but not on an energetic razor-edge), they can likely achieve sufficient per capita food security to allow group-living much more readily than larger, sympatric hog badgers, which are solitary despite being a similar build to *Meles*. In this regard, the tertiary role of winter torpor and/or hibernation seems quite variable (mitigating constraint 2). This trait is less useful in (sub) tropical regions, although curiously, while hog badgers do hibernate, the Chinese ferret badger does not. And while we might postulate that the latter perhaps are too small to do so effectively (Noonan et al. 2015b), winter torpor is a feature of skunk biology, likely exercised also by stink badgers, which are a similar size to ferret badgers, and also occupy tropical regions.

One factor we have not been able to cover in its entirety here is the extent to which intraguild competitors (constraint 3) might also impact the food security and thus ability to form groups among Asian badger species. In many European countries, aside from red foxes (*Vulpes vulpes*), there is little competition within the badgers' omnivorous guild, whereas in tropical regions there can often be a substantial array of niche competitors (see Y. Zhou et al. 2013a; Ross et al., Chapter 14, this volume).

We thus elucidate how study of this badger clan has revealed factors relating to the paradigm of group-living. But, in so doing, we also expose knowledge gaps, which will be resolved as the fundamental biology of lesser-known species becomes better established. We also integrate new concepts into socio-ecological paradigm, particularly for non-collaborative group-living species; ideas that warrant exploration in other taxa.

One commonality between these diverse Asian badger species, as well as their occidental cousins, is that they generally fare badly in proximity to people, vulnerable to sett loss through urbanization, road traffic mortality, programmes to manage disease, and deliberate hunting and persecution. Sadly, these threats are prevalent in expanding Asian economies (Y. Zhou et al. 2013a; Z. Zhou et al. 2015a, 2015b, 2015c), where cultural and attitudinal change (Z. Zhou et al. 2014a, 2014b, 2015c) are urgently needed to safeguard biodiversity for the future. Most pressing is that despite clear and evident pressures, and unknown population densities (and thus data deficiencies), as yet (Table 13.1) only the Bornean ferret badger is listed as Endangered, and the greater hog badger as Vulnerable, on the (recently updated) International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (Version 2016.3), while only the honey badger is (at the time of writing) listed by CITES.

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