Musteloid sociality: the grass-roots of society

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Giant otter group. © F. Hajek

What is special about the Musteloidea?

The musteloids are a very varied superfamily, debatably monophyletic, and united through ancestors such as *Plesictis*, which lived 32.8–30.9 million years ago (Mya) (Sato et al. 2012; but see Flynn et al. 2005). Their phylogeny is detailed in Koepfli et al. (Chapter 2, this volume), but in summary these approximately 90 species (Macdonald et al., Chapter 1, this volume) encompass about 30% of extant carnivoran species, making them the most species-rich taxon within the Order Carnivora.

Only giant (*Pteronura brasiliensis*) and sea otters (*Enhydra lutris*) ordinarily exceed 20 kg, and many musteloids are very small (< 1 kg); *Mustela* species are the smallest members of the Carnivora, with adults regularly weighing < 40 g. In Macdonald et al. (Chapter 1, this volume) we saw that musteloid diversity spans semi-aquatic river otters to fully marine sea otters, whereas terrestrial forms exploit niches from tree-tops, for example the scansorial martens, to the extensive excavations of the fossorial badgers. No other carnivore taxon exhibits this breadth of ecomorphology, or exploits this diversity of ecotopes. In part, this span of ecologies is driven by the dietary variation within the group—exceeding that seen even in the Canidae (Macdonald et al. 2004a): from fiercely predatory polecats to adaptable, omnivorous raccoons *Procyon* spp.; from piscivorous otters to the sweet-tooth of honey badgers *Mellivora capensis*; and to those species, such as kinkajous *Potos flavus*, with a penchant for fruit. Due to their trophic diversity and adaptability, musteloids are represented across all latitudes spanning every continent, bar Antarctica; from the wolverines *Gulo gulo* of the arctic tundra to the coatis *Nasua* spp. of Central and South America.

Insofar as carnivore society is a product of their ecology (Macdonald 1983), we begin this chapter with an expectation of encountering diverse societies. We ask what unifying themes are apparent in the behavioural ecology the musteloids, and how these transcend their societies.

We begin by expounding on the evolutionary history of the taxa, detailing how a spell of serendipitous climate change around 30 Mya 'thrust opportunity into the jaws' of early musteloids. We then move to the influence of ecological mechanisms on musteloid socio-spatial geometries, considering how species organize themselves with respect to diet, prey types, and the dispersion of resources, where group-living is rare within this super-family. Related to this, we investigate the role natal dens can play in promoting philopatry in a subset of species, provided they consume food types with the dispersion characteristics able to sustain maternal-offspring groups. Nevertheless, in all but a few musteloids, the drive to mate independently tends to terminate this nascent society, or force reproductive suppression.

From socio-spatial organization we elaborate implications for mating systems linked to a variety of reproductive specializations, in turn feeding back into their societies. We note strong (male biased) sexual size dimorphism (SSD) among especially the small, carnivorous mustelids, with decreasing extents of SSD with increasing body-size within this super-family.

Having contextualized musteloid societies (*sensu* Eisenberg 1966), we discuss the implications, adaptive benefits (or lack thereof) and consequences of the different extents of gregariousness apparent across species. But we commence here, at the beginning; looking for clues as to the roots of musteloid societies in their origins.

Evolutionary origins

'The present is the key to the past' (Lyell 1830), and arising from this uniformitarianism we seek understanding of contemporary musteloid societies through an examination of their paleontological history. The full phylogenetic evolution of the musteloids is expounded by Klaus-Peter Koepfli and co-authors in Chapter 2 of this volume, but here we briefly explore how two foremost ecological drivers—climate (Newman et al., Chapter 21, this volume) and habitat change drove their emergent socio-ecology. This occurred through two bursts of diversification, mostly in the Old World, in ways that have their roots in the evolution of grass

and grasslands; a product of the tectonic movement of Antarctica to the southern pole.

The first bout of diversification occurred around 33.5 Mya when, after the warm and stable 'Eocene Climatic Optimum', a 'Grande Coupure' (great break; Costa 2011; linked to the Mongolian faunal remodelling in Asia, see Meng and McKenna, 1998) in ecosystem continuity occurred, as Antarctica drifted to the south pole, driving global cooling linked to decreasing CO_2 levels (Prothero and Berggren 2014). Reduced atmospheric CO_2 favoured plants using C4 photosynthesis (Ehleringer et al. 1997) (a mechanism found only in angiosperms, predominantly Poaceae grasses). Consequently, forest ecosystems, abundant in the Middle-Eocene to late Eocene, transitioned to dry woodland, then to early Oligocene wooded grasslands, causing the extinction of 60% of terrestrial mammals (Prothero and Heaton 1996). But, as a corollary, in the mid-Oligocene a new biome emerged—grassland (Prothero and Berggren 2014). Ungulates grazing these grassy plains grew large, and so did the carnivores that hunted them; evolving to become fleet-footed pursuit predators. In contrast, smaller rodent herbivores, burdened by heat-loss and racing metabolisms, used their diminutive size to their advantage by hiding in the grass sward and seeking subterranean refuge in tunnel systems (Nevo 1999; Noonan et al. 2015a). This enabled rodents to evade both predators and climatic extremes (Ebensperger and Blumstein 2006), typically coping with the difficult digestion of grass through coprophagy. The pursuit of these small prey was to become the domain of a second adaptive strategy amongst the nascent Carnivora, exemplified by diminutive species such as *Palaeogale*—a cat-like creature weighing around 1 kg—which emerged as musteloid ancestors approximately 32.4–30.9 Mya in Asia (Sato et al. 2012).

These early carnivoran ecomorphs evolved to pursue rodent prey underground (Noonan et al. 2015a), according to two trajectories: the evolution of (and we opt for descriptive sobriquets) 'skinnymorphs' (weasel-type) and 'musclimorphs' (badger-type); a fundamental dichotomy of ecomorphological types that persists to this day (Friscia et al. 2007). The ancestral musclimorphs included species much larger than today's badger-types, for example, *Megalictis* (the giant weasel, reaching 60–100kg) and *Melodon* (the first ancestral badger, ca. 70kg) (Peigné et al. 2006). These evolved forelimbs suited for digging (see Andersson 2004; Kitchener et al., Chapter 3, this volume) and ripped open rodent burrows. By contrast, skinnymorphs evolved to slip into rodent burrows to capture

prey—a vivid example is provided by entombed fossils of the proto-mustelid *Zodiolestes* (Martin 1989) wedged firm in the evocatively named 'devil's corkscrew' burrows of the Miocene burrowing beaver *Palaeocastor* that they preyed upon.

The second bout of musteloid diversification occurred around 5 Mya, with further cooling during the Pliocene (producing current patterns of seasonality; Klotz et al. 2006) driving diversification and radiation of rodent (and passerine) prey (Koepfli et al. 2008a). A sub-set of mustelids predating on small rodents underwent more extreme selection (King and Powell 2007), down to species weighing <100g such as *Mustela praenivalis*, capable of chasing cricetid rodents through sub-nivean tunnels. It was also around this time that musteloids radiated into South America, with the formation of the Panamanian land bridge (Sato et al. 2012).

Of course, while this musclimorph/skinnymorph dichotomy emphasizes the grass-roots of musteloid ecology and society, it also simplifies them; there were also, for example, 'aquamorphs': sinuous ancestral otter forms, such as *Enhydriodon* spp. Similarly, others diverged from hunting small vertebrates to more generalist, omnivorous diets including insects and fruit in trees; for example, *Pseudobassaris riggsi*, the first stem procyonid (with the tell-tale suprameatal fossa in the temporal skull bone—see Wolsan and Lange-Badré 1996) appeared 30.3–27.6 Mya; procyonids proper emerging in the Eurasian Oligocene (see Koepfli et al., Chapter 2, this volume).

'Paws' for thought

Pivotal to this emerging synthesis, is that adaptations suited to running prove incompatible with being adept at other lifestyles, and vice versa. As Andrew Kitchener et al.'s chapter on form and function (Chapter 3, this volume) explains, the musteloids tend to have a much more plantigrade stance than the felids or canids, for which digitigrade feet extend limb length, enabling a longer running stride. It is musteloids' broad paws, however, that provide such a good template for webbing, aiding the otter's swim stroke, or enabling badgers to dig so powerfully, or providing 'snow-shoes' to the wolverine. Long claws also hamper running, and thus while cats retract their weaponry, and dogs make do, freed from design limitation the musteloids exhibit elaborate and highly adapted claws, from the climbing hooks of procyonids to the digging tines of badgers. Musteloids thus exhibit substantially more paw variation than any other carnivore family, from the walloping pads of wolverines, to the near primate-like phalanges of kinkajous and olingos (*Bassaricyon* spp.), to the refined fore-feet of the non-piscivorous otters. Not forgetting the red panda's (*Ailurus fulgens*) 'thumb' (actually formed by its radial sesamoid wrist bone).

Using these paws effectively requires often highly flexible wrists and particularly tough humeri and short limbs that are anatomically maladapted to running—where no other carnivore family exhibits such diversity. The gait of small, flexible, elongate musteloids, and especially semi-aquatic species, tends to skip straight from walking to bounding, without the efficient trot benefitting the running guilds (Kitchener et al., Chapter 3, this volume). While some larger musteloids can trot, their need to grip objects with their forelimbs, to climb, or to pull up rocks, requires a degree of limb abduction than would be unstable for accomplished runners. In general, forelimb supination becomes increasingly at odds with relaxed running costs (Kram and Taylor 1990) as body size increases (Andersson 2004). Similarly, hip and ankle morphologies have evolved to suit these various, non-running, modes of life exemplified by the musteloid.

And these constraints of anatomy are not just present day, practical limitations. In a meta-analysis across the Carnivora, we (Noonan et al. 2015a) identified substantial phylogenetic inertia in these ambulatory traits. Indeed, ichnofossil evidence of burrowing behaviour (as distinct from den use) suggests that ancestral felids, procyonids, and viverrids evolved along trajectories incompatible with digging (Macdonald 1992; Andersson 2004); whereas digging adaptations are apparent in the amphicyonid bear dogs (Hunt et al. 1983), *Zodiolestes* spp. (Martin 1989), and the giant mustelid *Megalictis* (Hunt and Skolnick 1996).

Evolved sociopathy?

This excursion into musteloid phylogeny may also have bearing on a trait for which they are renowned: 'ferocity'. Indeed, the mustelids include some of the carnivores most renowned for their relentless formidability: honey badgers are apparently 'devoid of fear' in the face of leopards *Panthera pardus*; wolverines stand firm against cougar *Puma concolor* and bear *Ursus* spp; and American badgers *Taxidea taxus* repel coyote *Canis latrans* bands. Indeed, the BBC (2007) reported that residents of Basra believed the British army was secretly releasing honey badgers as a [quote]: 'Man eating weapon to subdue the populace'. That musteloids can punch above their weight against larger guild competitors is also invoked to explain the evolution of the

aposematic 'war paint' worn by many (Newman et al. 2005), augmented by toxic stench in some (Stankowich et al. 2011; see Buesching and Stankowich, Chapter 5, this volume).

This ferocity might even exert limitations on the sociability of musteloids, through eco-physiological inertia. Catecholamines (notably adrenalin/epinephrine that drives the stress response; Selye 1936) are normally oxidized speedily. A common male mutation in humans, however, causes the inhibition of monoamine oxidizing genes and is associated with the so-called 'warrior' personality type (McDermott et al. 2009). Might the fierce mustelids carry phylogenetic ferocity? Notably too, many musteloids—badgers, raccoons, martens—sleep their way through famine using adaptive torpor (something no felid does, and only raccoon dogs amongst canids), relying upon high levels of the hunger-alleviating hormone leptin in order to do so (Rousseau et al. 2003; Mustonen et al. 2006). This very same hormone stimulates catecholamine secretion (Takekoshi et al. 1999)—thus we speculate (Noonan et al. 2015a) that biochemical pleiotropy might foster fearlessness. In a similar vein, oxytocin, the affection or 'anti-psychotic' hormone (Magon and Kalra 2011; Rubin et al. 2014), must be inhibited for delayed-implantation (Douglas et al. 1998); which is another musteloid hallmark (we discuss later), again to the detriment of an affectionate nature (Caldwell et al. 2008).

So we see that climate and habitat change drove grassland to develop, and in turn that the pursuit of rodent prey invading these grasslands was vital to the evolution of the ancestral musteloid blueprint. These rodent prey tend to be sparse, homogeneous, slowly renewing, and must be secured through defence,

setting the baseline for individual intrasexual territories in the carnivorous musteloids (Powell 1979a). This observation launches the ecological-energetics argument that we next unfold, explaining how diet and prey size relates to prey dispersion characteristics, and how this can dictate home range overlap linked to spatial group formation.

Drivers of musteloid socio-spatial organization

Energetic constraints: small prey and how best to catch them

Understanding the role played by diet, and the exploitation of resources (Macdonald 1983), has proven key to unlocking mammal societies (Macdonald and Johnson 2015). We will elaborate cases involving various diets, below; however, the relationship between predator size and prey size has proven fundamental among carnivores. From Figure 6.1, we observe, unsurprisingly, that larger carnivores eat larger prey. Notably, however, while small carnivores can make their energy budgets balance by eating very small prey, species over a 14–20 kg threshold need to eat much bigger prey (Carbone et al. 1999, 2007). In our previous work, this discontinuity has proven revealing in categorizing the societies of both canids and felids (Macdonald et al. 2004a; Macdonald et al. 2010b).

Canids essentially evolved for fleet-footed predation (subsidized by omnivory), where the constraints of over-heating placed a ceiling on maximum body size—such that the largest extant canid long-distance pursuit hunters (grey wolves, *Canis lupus*, male ca. 50–80 kg)
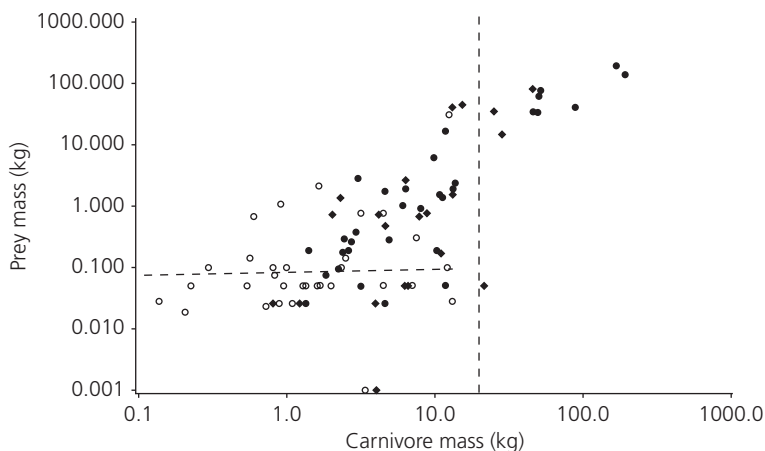
Figure 6.1 Prey mass trends with body size for musteloids (open points), felids (closed points), and canids (diamonds). Vertical reference line denotes the discontinuity identified for carnivores as a whole by Carbone et al. (1999) at *c.*20 kg. Data from Carbone et al. (1999). Best fit line for musteloids excludes the outlying wolverine point.

are substantially smaller than the largest stalk-pounce felids (tiger, *Panthera tigris*, male ca. 200–300 kg). To solve this thermodynamic problem, they instead evolved collective packing power, exemplified by the co-ordinated hunting strategies of wolves (Schmidt and Mech 1997). Furthermore, through the fission and fusion of these packs, canids can shift their collective body-mass to enable them to escape the exponent of prey–predator size, and thus also still eat smaller prey when hunting individually, or shift to omnivory, under appropriate trophic resource conditions (Macdonald et al. 2004a). Amongst the felids (Figure 6.1), selection for greater individual body-mass is evident, where, through stealth, a powerful bite is delivered best by massive force (Macdonald et al. 2010b).

A similar exploration of musteloids, however, exposes a different reality; for this group predator size does not scale with prey size (Figure 6.1), not least because all extant terrestrial musteloid species weigh less than the 20kg cut-off, shown by the vertical dotted line in Figure 6.1. This was also the case for many of their ancestors; where even the larger ones excavated small(ish) rodent prey, and, of the aquatic musteloids, giant- and sea-otters are limited to body masses < *c*.35 kg (doubtless bumping their heads against the glass ceiling of competition with the seal super-family).

Among the musteloids, a few mustelids can take prey much bigger than themselves: a 250 g stoat (*Mustela erminea*) can kill a 2.5 kg rabbit *Oryctolagus cuniculus* (Day 1968), a 1.5–2 kg sable *Martes zibellina* can kill a 10 kg musk deer *Moschus moschiferus* (Monakhov 2011), and a 15 kg wolverine can, through ambush in deep snow, kill a 75 kg reindeer *Rangifer tarandus* (Andren et al. 2011). But the wolverine is an exception—most musteloids weigh less than 10 kg and exploit prey below 1 kg. We note that Kruuk and Mills (1983) consider Stevenson-Hamilton's (1947) claim that honey badgers predate on buffalo (*Syncerus caffer*) and blue wildebeest (*Connochaetes taurinus*) by biting at their testicles to be apocryphal. The non-mustelids in the super-family eat smaller prey than do the mustelids. Overall, in contrast to the canids and felids, we see no correlation between musteloid body mass and characteristic prey size: if we consider the mustelids alone, the slope would be essentially zero (the near horizontal dotted line in Figure 6.1). Some species, however, have such a varied diet that it is hard to assign characteristic prey size. That difficulty notwithstanding, we can see that, in clear contrast to the canids and felids, the tendency to eat proportionately smaller prey occurs predominantly in the larger musteloids (Figure 6.2, the wolverine being a clear outlier from this trend).

These allometries reflect that due to surface area to volume scale laws (LaBarbera 1989), the small lithe physique of skinnymorphs (King and Powell 2007), moulded by their subterranean/-nivean capabilities, are energetically inefficient. Inevitably, balancing energy budgets is particularly challenging for these small mustelids in winter, when rodents become scarcer and other food types, such as fruit and invertebrates, cease to be available outside of the tropics (e.g. Zhou et al. 2011b). Consequently, the smallest musteloids (<1 kg) are so expensive to run that they have little option but to eat calorically dense, protein-packed vertebrate prey (Moors 1977). For example, when it is cold, the metabolic rate of the elongate *M. freneta* (*c*.150–300 g) is 50–100% higher than that of a 'normally' shaped mammal of the same weight (Brown and Lasiewski
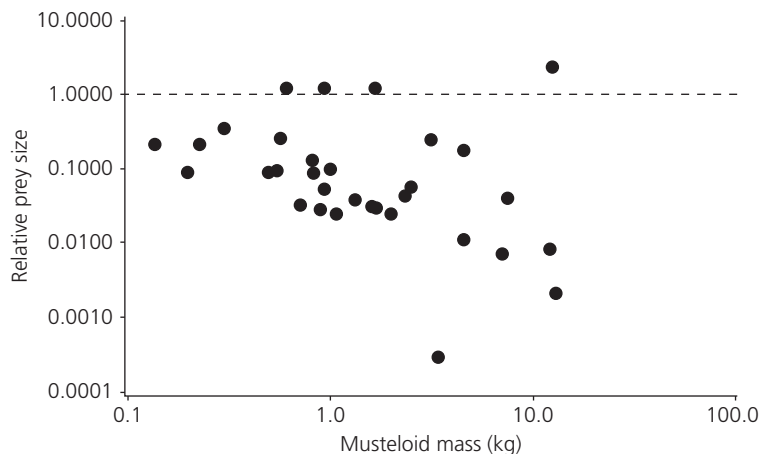
Figure 6.2 Characteristic relative prey size and musteloid body mass. Slope is 0.37 on a log-log scale, CI ± 1.20, without the inclusion of the wolverine (outlying point in upper right quadrant).

1972). For the more rotund musclimorph mustelids, different strategies are possible: while wolverines can kill reindeer, the morphologically similar European badger forages *Meles meles* mostly for earthworms. Furthermore, these heavier forms often use torpor and denning to reduce their metabolic demands (Newman et al. 2011; Zhou et al., Chapter 13, this volume).

While prey–predator size relationships had sociological ramifications for the evolution of canid and felid societies, there is no evidence amongst the predatory terrestrial musteloids for selection for larger body size, or pack-formation, to tackle larger prey. Why not? As discussed, one answer might lie in a combination of phylogenetic baggage (inertia) and guild structure, where many musteloids are poor runners (see Andersson 2004). As a consequence, any attempt to embark on a trajectory to become larger stalkers or runners might have run into a monopoly imposed by the cats, dogs, and hyaenas, already masters of those arts. Related to this, arboreal and subterranean ecotopes are not realms occupied by large prey, due to physical constraints imposed by gravity and soil cohesion, respectively (Noonan et al. 2015a), and so solitary individuals can hunt effectively.

Prey type and dispersion

The small vertebrate prey that very small mustelids rely upon tend to be homogenously dispersed and thus divisible into discrete territories, each sustaining a single individual. Consequently, an over-arching pattern emerges, such that the greater the contribution small mammals make to their diet, the more solitary and less sociable musteloid species tend to be (Johnson et al. 2000). However, many musteloids eat few, if any, rodents, favouring instead frugivorous and insectivorous diets, often linked to opportunistic omnivorous generalism (e.g. Zhou et al. 2011b). For example, *Martes* spp. (martens), *Meles* spp. (old world badgers), *Procyon* spp. (raccoons), *Bassariscus* spp. (ringtails), *Potos flavus* (kinkajou), *Bassaricyon* spp. (olingos), and *Ailurus fulgens* (red panda) consume significant seasonal proportions of everything from insects, worms, molluscs, eggs, fruits, seeds, and nuts, through to cereal crops, and even honey. These food types, along with the fish eaten by piscivorous otters (Lutrinae), tend to be locally abundant and rapidly renewing, constituting clumped, widely dispersed resources. Associated with this is that although no terrestrial, predatory musteloids live or hunt in adult packs, several species consuming diversified food types do form groups, with

varying degrees of permanence. So this leads us to probe how diet interacts with social organization.

As a generalization, greater prey abundance per unit area (of which only a proportion may be available) equates to a higher environmental carrying capacity, leading to higher population densities and, *pro rata*, smaller individual ranging areas (Macdonald 1981; Gittleman and Harvey 1982; Reiss 1988; Powell et al., Chapter 11, this volume). Variation in the availability and distribution of food resources (as well as other resources, such as mates and dens) can influence tolerance of conspecifics, and, in circumstances where the net marginal benefits of mutual associations exceed the costs of competition (Alexander 1974), group-living is favoured (Macdonald and Carr 1989; Kokko and Rankin 2006; Silk 2007; Cameron et al. 2011; Huchard and Cowlishaw 2011). Furthermore, while some musteloids—notably the lutrines (Groenendijk et al., Chapter 22, this volume) and certain procyonids (Hirsch and Gompper, Chapter 28, this volume; Brooks and Kays, Chapter 26, this volume)—display a repertoire of social behaviour associated with group-living, paradoxically, in other less obligate group-living species, the absence of cooperative behaviour is conspicuous (Macdonald 1983; Kruuk and Macdonald 1985; Woodroffe and Macdonald 1993), exemplified, as we will see later, by European badgers (Macdonald et al. 2015b).

The Resource Dispersion Hypothesis

A key concept that unifies how diet and food dispersion can leverage home-range overlap took shape in 1974 when one of us, DWM, and his then mentor, Hans Kruuk, made some nocturnal scribbles (quite literally on the back of an envelope), that developed into what subsequently became formalized as the 'Resource Dispersion Hypothesis' or 'RDH' (see Macdonald and Johnson 2015). The RDH states that groups can develop where resources are dispersed such that the smallest economically defensible territory for the primary occupant(s) can also sustain additional animals (Macdonald 1983). At its simplest, patch dispersion determines the size of territories, and patch richness determines the number of individuals that can viably cohabit the territory; insofar as patch richness and patch dispersion are independent, larger groups need not necessarily maintain larger territories (e.g. Macdonald 1983; Carr and Macdonald 1986). The RDH explains how spatial congruity can arise from selective pressures in the absence of any sociological benefit of

cooperation (Carr and Macdonald 1986). As a consequence, purely ecological conditions can facilitate cohabitation of a territory, resulting in group-living in a minimalist form, termed 'spatial groups'.

A basic tenet of the RDH is that all group members must be able to maintain their minimal food security requirements (Carr and Macdonald 1986; Blackwell and Macdonald 2000; Johnson and Macdonald 2003; Newman et al. 2011). Importantly, the larger the absolute value of the food security demanded by the primary territory occupant(s) (typically the mother of a philopatric litter, and the associated father) and the lower the requirements of the secondaries, the more likely it is that secondaries can be accommodated (and, in practice, these are most likely to be retained young; see Kaneko et al. 2014; Noonan et al. 2015a). Of course, smaller, juvenile animals may also be most susceptible to interrupted food supply, and thus set the threshold of what level of conspecific tolerance that species can tolerate (Groenendijk et al., Chapter 22, this volume; see also Newman et al., Chapter 21, this volume). Again, the fact that many musteloids are 'skinnymorph' is relevant here. Those species with a morphology suited to agility and/or scansoriality tend not to have substantial fat reserves, especially if they are small. Contrasting solitary *Martes* spp. with more social *Meles* spp. (Zhou et al., Chapter 13, this volume), Newman et al. (2011) posit that because martens carry much less reserve fat than do badgers, they are less able to tolerate extended periods without feeding, and thus less able to form groups despite, in most instances, both genera eating a similarly omnivorous diet.

The RDH and musteloid societies

European badger society has been used extensively to investigate the paradigm of how resource dispersion favours group-living. This is largely due to the badgers' primary food source, the earthworm (*Lumbricus terrestris*) having availability, dispersion, and patch richness characteristics fitting with the shareable and indivisible predictions of the RDH (see Macdonald et al. 2015b). Worm-rich feeding sites are uneconomic for an individual badger to defend because when worms surface they are super-abundant; compounded by the indefensibility of the wide variety of other food sources consumed by these adaptable generalists. As predicted by RDH theory, this leads to overlapping territories, where—as we shall discuss later—shared (originally natal) dens (termed 'setts') further enhance congregation. Further testing these tenets of the RDH

and fossoriality, in Chapter 13 of this volume, Youbing Zhou and colleagues examine the societies of various badger (and loose associate) species throughout Asia. They corroborate that a trend for omnivory in this group is the primary precursor of group-living, noting more carnivorous badger species are solitary.

Another musteloid species for which trophic resource dispersion facilitates extensive home range overlap is the kinkajou (Kays and Gittleman 1995; Kays 1999a; Kays et al. 2000; Kays and Gittleman 2001). In Chapter 26 of this volume, Melody Brooks and Roland Kays describe not only social units comprised by one adult female, her pre-dispersal offspring, and two adult males, but also that kinkajous spend around 20% of their time feeding together in troops in large fruiting trees (although they travel and feed singly when feeding on the fruit of small trees). The larger the feeding tree, the larger the group. Here, which tree is in fruit is the ephemeral food patch, where large trees can yield a super-abundant food supply. Groups also consolidate at denning sites, where group-members allo-groom and mutual scent mark (Kays and Gittleman 2001). In contrast, slender yellow-throated martens *Martes flavigula*, which also feed extensively in the crowns of sub-tropical fruit trees but are less able to tolerate compromised food security, neither feed nor den in groups (Zhou et al. 2008a; 2011a). As well as consuming fruit, yellow-throated martens also actively hunt vertebrate prey, exemplifying how the resource-scape interacts with diet, where inability to share resources can reduce individual food security and limit some species to more solitary social systems (Newman et al. 2011).

As Ben Hirsch and Matt Gompper describe in Chapter 28 of this volume, the white-nosed coati *Nasua narica* is seemingly unique within the Carnivora in maintaining a dichotomous social structure with group-living females and solitary males (34% larger than females) (Gittleman 1989; Gompper 1995; Kaufmann 1962). Groups (called bands) comprise from six to over 30 related and unrelated females and their immature offspring (Gompper 1994, 1996). These female bands and their dependent offspring are highly social (Gompper 1994). Despite this, coati bands are not harem groups; all adult males remain solitary with the exception of a brief (approximately two-week) synchronous breeding season. Individual fruiting trees are rich, shareable, and not readily divisible food patches, where larger males would out-compete smaller females unless they formed coalitions. In Mexican tropical dry forests Valenzuela and Macdonald (2002) studied white-nosed coatis at two sites that were broadly similar, with

marked seasonal rainfall, but had contrasting resource abundance and dispersion characteristics. The home-ranges of seven bands varied in extent between 45 and 362 ha, determined by the dispersion of water sources during the dry season (patch dispersion); although this resource was—as one might expect—unrelated to group sizes; that is, water has no real 'richness'. Female coalitions benefit from vigilance; at a waterhole in Palo Verde, Costa Rica, Burger and Gochfeld (1992) observed that coatis came to drink singly or in groups of up to 13; however, it was only males that came to the waterhole alone. Coatis in larger groups drank for longer, and were individually less vigilant and remained at the waterhole longer than did smaller groups.

In line with Emlen and Oring's (1977) proposition that the drivers of society differ between the sexes, working with Yayoi Kaneko (Kaneko et al. 2014), our team found that in a population of Japanese badgers (*Meles anakuma*) living at a density of 4 individuals per km^2, the average home range size of males expanded from 33.0 ± 18.1 ha in the non-mating season to 62.6 ± 48.2 ha in the mating season, and was significantly larger than the more consistent range size of 15.2 ±6.3 ha recorded for females. Females with cubs had home ranges exclusive of other adult females, configured around areas rich in food resources, indicative of intra-sex territoriality. This exemplifies how the constant territory size hypothesis (CTSH; von Schantz 1984a; 1984b; 1984c), interacts with the RDH. The CTSH identifies an 'obstinate strategy'—evidenced if individuals adopt a territory size adjusted to its needs during low resource availability periods—and a 'flexible strategy', where territory size varies seasonally with resources (e.g. access to females for males).

Similarly, in Chapter 18 (this volume), Jeffery Copeland and colleagues describe how male wolverines increase their home range size and roaming behaviour during the mating season. While female wolverines have intra-sexual exclusive territories (to ensure they reliably sequester adequate resources to provision their offspring), males exhibit around a 16% intra-sex range overlap. This reconciles with Vangen et al. (2001) who propose that, in accord with RDH concepts, the spacing of female wolverines is determined by the abundance and dispersion of food, whereas the distribution of males is determined by the distribution of females, at least in the breeding season. Although many smaller, solitary, carnivorous musteloids follow a similar intra-sex territorial pattern (Powell 1979a; Erlinge and Sandell 1986), for the larger wolverine Copeland et al. posit that in years with good prey availability, juveniles and

sub-adults can remain associated with the maternal den and their parents' territories; corroborating the predictions of Noonan et al. (2015a) on how dens act as foci in RDH marginal species.

Raccoon society provides a dynamic and varied model for how resources can dictate the advantages to social aggregation under suitable conditions. Raccoons form transient fission–fusion coalitions, with many short-term acquaintances and a few long-term associations. Here again, the extent to which food is clumped and divisible is crucial in determining their social system. In an insightful feeding experiment, Morgan Wehtje and Matt Gompper (2011) compared home-range size, two-dimensional overlap, and volume of intersection (VI) values between 22 raccoons with access to clumped food resource (site A) and 19 raccoons at an adjacent control site (B) that received similar food quantities, but where food was distributed in a non-clumped and spatially–temporally unpredictable pattern. There was no difference in home-range size between the two sites, nor any inter-sexual difference in home-range size. The animals at site A, however, exhibited two-dimensional home-range overlap values and VI scores that were nearly twice those of raccoons inhabiting the control site B. Wehtje and Gompper (2011) concluded that these differences appeared to be driven by increased overlap among females at the experimental site A, because males from the two treatment sites had similar home-range overlap and VI scores. Similarly, in urban parks, skunks remain solitary (foraging on mowed lawns, presumably for insects), but raccoons aggregate, around rich food clumps (rubbish bins) (Prange et al. 2004; Rosatte et al. 2010; see Macdonald et al., Chapter 1, this volume).

Moving to the aquatic environment and a piscivoran diet, working with coastal Eurasian otters (*Lutra lutra*) in Scotland, Kruuk et al. (1989) and Kruuk and Hewson (1978) found solitary males fished diurnally and occupied large, 2.7–4.5 km linear territories, usually comprising a strip within 100m of the shore. These territories overlapped several groups of territorial female otters, comprising 2–5 individuals, of which several, or all, bred each summer. This distribution pattern equated to spatial groups, within which group members operated separately (in fact they spent more than half their time in individual core areas). Female groups were configured around fresh water and rich fishing patches, which in RDH terms were both indivisible and shareable. In these cold waters otters must maintain very high metabolic rates in order to keep warm. In water of 10°C, an otter needs to catch 100 grams of

fish per hour for three to five hours a day in order to survive; nursing mothers up to eight hours. This places severe constraints on achieving minimal food security, where females tolerated conspecifics only provided they were able to maintain enough reliable access to food most of the time. By contrast, males need access not just to food resources, but also to females. Consequently males sometimes expanded their range to encompass more than one group of females.

In Chapter 22 (this volume), Jessica Groenendijk and co-authors describe an extreme form of sociality among giant otters (*Pteronura brasiliensis*) in Manu National Park, Peru. These live in groups varying from a pair to extended families of up to 13 individuals, each only including a single breeding male (Groenendijk et al. 2015b). Here, the RDH pertains to the availability of fish, which are particularly numerous in ox-bow lakes, with just two species of fish comprising over 70% of the giant otter's diet. Studying a population segregated into 12 territories, Groenendijk et al. found each to encompass one or more lakes, together with associated rivers and swamps. These territories overlapped, but their cores (the lakes) were exclusive, acted as patches of super-abundant food that could be shared between conspecific residents, and were almost certainly defended. Consequently, according with the effect of patch richness, territories with larger cores supported more populous groups, while territories with smaller cores supported only breeding pairs. And in the Biblical vein of: 'To them that hath shall be given' (Mark 4.25), larger groups produced proportionately more cubs annually, and these were more likely to disperse successfully. Recruitment of offspring into the adult population was greater in years when a territory included more non-breeding helpers. Why are the lakes not sub-divided among two or more territories? We suspect that the cost of competing with other groups to defend an irregularly shaped fraction of a lake is unsustainably high. More effective is for a group, or even a pair, to hold exclusive dominion over a lake and, when they have secured that lake, they may be able to recruit additional members into their lake group and thus derive enhanced cooperative benefits while maintaining sufficient individual food security. Because all lakes tend to be occupied, there is a lack of dispersal opportunities, which tips the cost–benefit calculus for any cub in favour of 'staying at home'; particularly in territories with greater carrying capacity.

Research on African clawless otter (*Aonyx capensis*) also illustrates how spatial groups form under certain food dispersion conditions. Somers and Nel (2004) found that total home range length correlated with mean reed bed (a high density food patch) nearest neighbour distance, leading to female range overlap, in accord with RDH predictions. Mason and Macdonald (2009) also report maternal-offspring groups in African clawless otters. Similar mechanisms might also explain groups of up to four female hairy-nosed otters (*Lutra sumatrana*) in Cambodia (Long 2000; Poole 2003). It was this type of system that was anticipated by Rowe-Rowe (1977), when he proposed that sociality in otters may have arisen almost by default, there being no selective pressures against group foraging, particularly on crabs or in muddy rivers in the tropics. Asian small-clawed (*Aonyx cinereus*) and smooth-coated otters (*Lutrogale perspicillata*) are unusual among musteloids in that they form monogamous pairs, although groups can occasionally arise, temporarily, through natal philopatry. Family groups are also sometimes (though not always) observed in spotted-necked otters (*Hydrictis maculicollis*). North American river otters (*Lontra canadensis*) are more social still, where a female and her philopatric progeny form maternal-offspring groups, and, although males disperse from such family groups earlier than females (resonating with Japanese badgers; Kaneko et al. 2014), groups of over 10 adult males have also been observed. These males do not seem to be territorial and remain gregarious even through the mating season (Hansen et al. 2009). In contrast, while rafts of sea otters *Enhydra lutris* might look like social groups, like badgers, these individuals feed independently, and groups are single-sex (see Estes et al., Chapter 23, this volume).

Collectively, these examples show that the distribution of resources can affect spatial overlap among individuals substantially, even when the mean home-range size of the population does not change. This further illustrates that while a site's overall resource availability influences population size, the spatial clumping of resources can facilitate the formation of, minimally, spatial groups, but often with more entwined social interactions.

Home range scaling and overlap

Turning to home range overlap, we have established that when prey can be partitioned into one-animal helpings carnivorous musteloids generally segregate into separate territories, where larger male territories overlap those of females (Powell 1979a). We have also established that when resource dispersion no longer renders individual territories the most efficient socio-spatial geometry, home range sharing results. So how do

musteloid home ranges scale across the striking range of body size that occurs across the super-family, and what does this spatial geometry mean for their society?

All else being equal, the greater metabolic demands of being larger lead to the expectation that home ranges should scale with body mass to the power of 0.75 (McNab 1963). The expected scaling is not 1.0 because larger bodies have lower surface area to volume ratios, which reduces the rate of heat loss, and thus overall energy requirements (LaBarbera 1989). In reality, across a wide range of taxa and types of feeding ecology, home ranges actually scale with body mass with an exponent consistently higher than 0.75 (Glazier 2005). For the musteloids as a whole, the scaling exponent is close to 1.0 (Figure 6.3). The reason why is not well understood, but there is an inevitable tendency for larger ranges to overlap more (Jetz et al. 2004). For some carnivores, but not the musteloids, the tendency of large prey to herd together may also be a factor (Carbone et al. 2007).

The different intercepts for best fit lines corresponding to the points representing the families in Figure 6.3 illustrate how, for a given body mass, the mustelids tend, as a group, to be more reliant on dispersed small rodents and have larger (on average) home ranges than do other musteloid families. Re-examining data from Johnson et al. (2000) for 20 mustelid species where both female mass and home range size were known, a more complicated picture emerges; that is, variation in social system as a likely consequence of food dispersal appear to be influential.

We classified social systems into four types: solitary (13 species), pairs (1 species), variable groups (5 species), and groups (1 species, giant otter). The scaling of home range with group mass is clearly different for solitary species compared with other social systems (Figure 6.4). Furthermore, group-living species stand out as having smaller home ranges, relative to their body size (Figure 6.4).

The group-living European badger, and both the giant otter and sea otter, lie well below the best fit line for solitary species. Diet comprised of small prey items occurring in rich patches, namely invertebrates, fish, and bivalves respectively, are probably responsible for these conspicuously small home ranges. Consequently, we observe that both the size of home ranges and the extent to which ranges can be shared by conspecifics depends on the quality and dispersal of resources; corroborating the RDH-based explanation of musteloid societies.

Musteloid societies, sexual dimorphism, and mating systems

One conspicuous aspect of musteloid biology is that, in common with many mammal species (Hedrick and Temeles 1989), males tend to be larger than females (Moors 1980; body size data in Macdonald et al., Chapter 1, this volume). In contrast to many Carnivora, however, the mustelids are particularly dimorphic, with sexual size dimorphism (SSD) ranging from parity up to males being more than twice the size of females. Indeed, this extreme sexual dimorphism is even apparent in the fossil record of musteloids, for example, *Aleurocyon, Megalictis*, and *Paraoligobunis* (Hunt and Skolnick 1996).
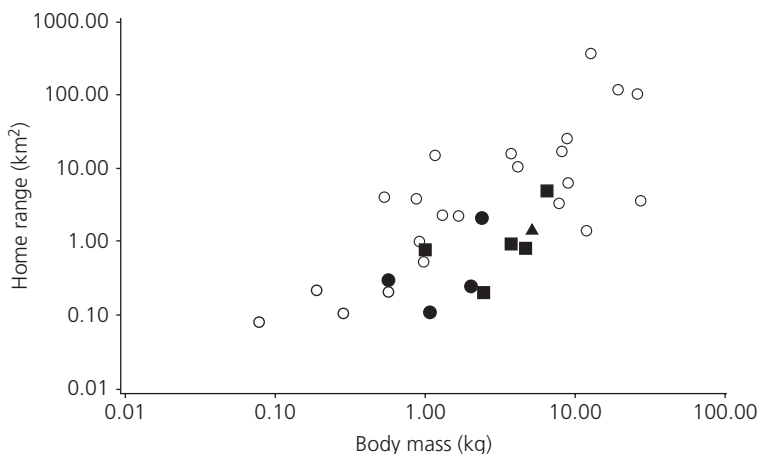
Figure 6.3 Scaling of home range and body mass in Mustelidae (open circles), Ailuridae (triangle), Mephitidae (filled circles), and Procyonidae (squares). The intercepts differ significantly among families ($F_{3,27}$ = 3.7, P = 0.03) but there is no evidence for a difference among slopes ($F_{2,25}$ = 0.02, P = 0.98). Common slope = 1.04 (SE = 0.17).
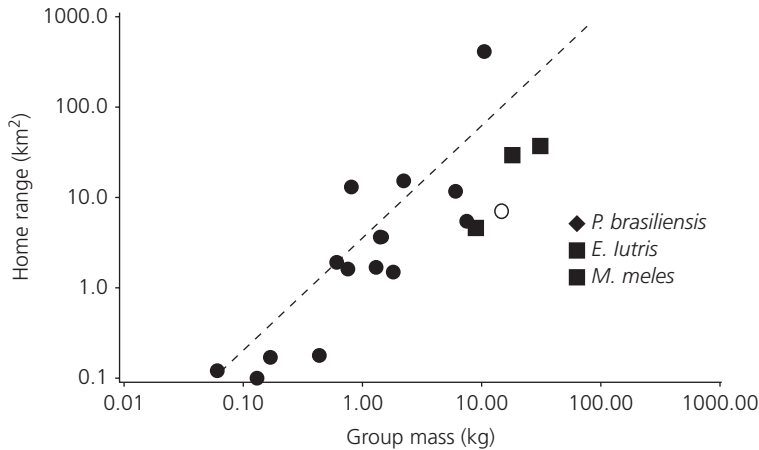
Figure 6.4 Scaling of home range with group mass for solitary (filled circles), pair-living (open circle), group-living (squares), and social (diamond) mustelids. Best fit line for solitary species shown (slope = 1.40, SE = 0.24). The scaling exponent was steeper in solitary species compared with the others (interaction term sociality*female mass $F_{1,15}$ = 11.30, P = 0.0043).

Early work speculated that SSD was a special case of character displacement (Hedrick and Temeles 1989 and references therein), with dimorphism serving to reduce competition for suitably sized prey types between sexes. In her meta-analysis, however, Fairbairn (1997) concluded that it is unlikely that inter-sex niche divergence plays more than a subsidiary role in the evolution of SSD (see also Gittleman and Van Valkenburgh 1997). Subsequent work has emphasized the importance of sexual selection, arising in polygynous mating systems because larger males are more competitive in terms of securing access to mates. In instances where females' mate choice is also influential, the prospect of larger, more competitive sons would be preferred, leading to positive sexual selection (Soulsbury et al. 2014). Indeed, sexual selection is

now the most widely accepted explanation of SSD in mammals (e.g. Isaac 2005).

The importance of sexual selection in maintaining male-biased SSD also underlies a proposed allometric pattern known as 'Rensch's Rule'. This rule states that, within a lineage, SSD is positively correlated with body mass in taxa where males are larger, and negatively correlated where females are larger (e.g. Abouheif and Fairbairn 1997; Fairbairn 1997; Dale et al. 2007; Sibly et al. 2012). In the Musteloidea, however, male-biased SSD clearly decreases with body mass (Noonan et al. 2016; Figure 6.5).

As we have just discussed, diet and trophic dispersion play central roles in determining how individuals organize their intra- and inter-sex territories (Powell 1979a; Johnson et al. 2000), and, crucially, optimize access to
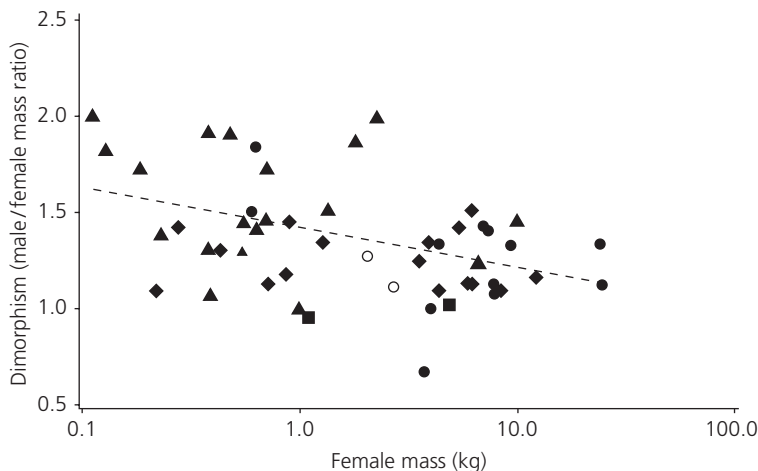
Figure 6.5 Trend in musteloid SSD and female mass indicating broad dietary classes: aquatic protein (closed circles), terrestrial protein (triangles), omnivores (diamonds), insectivores (open circles), herbivores (squares). Dimorphy is represented here as the ratio of male to female size as is conventional (with least squares fit line). As Fairbairn (1997) observes, the null hypothesis of no allometric trend is best tested by regressing male versus female mass (both on log scale) where a slope consistent with 1.0 indicates no evidence for allometry. We used the R (CRAN) MCMCglmm package (Hadfield 2010) to control for phylogenetic dependencies. For these data MCMCglmm slope CI = 0.88–0.99, indicating negative allometry.

mates (Weckerly 1998). Ralls (1977) speculated that the quality and dispersion of food resources could oppose polygyny—which facilitates selective mate choice—by influencing the dispersion of females. Indeed, our own recent study (Noonan et al. 2016) shows that SSD is greatest among carnivorous musteloids, followed by piscivorous, omnivorous, insectivorous, and herbivorous species, respectively (Figure 6.5). Furthermore, SSD was also influenced by social system, where the extent of dimorphism was greatest in solitary species, and least in group-living species.

Sexual selection, however, does not provide a complete explanation for SSD—it is also necessary to explain what determines female size. In cases of selection for larger males, there will also be selection for larger females due to direct genetic linkage (i.e. genes determining body size; Kemper et al. 2012) and indirect effects (i.e. females need to be larger to produce larger male offspring, Lindenfors 2002). Carranza (1996) reports that greater SSD is associated with smaller litter sizes in mammals, because fecundity decreases with increasing body size (Lindenfors et al. 2007). So, fecundity appears to be a balance between the dual influence of absolute female mass, and that relative to males. Furthermore, in those musteloids subject to selection for high fecundity, such as very small mustelids prone to r-selected mortality (Allainé et al. 1987; Healy et al. 2014), gestation and lactation place a great deal of stress on females (Gittleman and Thompson 1988). For instance, a female stoat weighing 150 g might give birth to a litter of up to 15 neonates, each weighing *c*.3 g (King 1983a). This 30 g litter (minus placental weight) would comprise 30% of her non-pregnant weight. In contrast, a female badger weighing 12 kg giving birth to maximum three cubs, each with a neonatal weight of 75 g, adds less than 2% of her mass (Larivière and Jennings 2009). Indeed, Moors (1980) demonstrated the energetic advantage of smaller female size for *M. nivalis*, where a lactating female requires about 20% less energy (equivalent to 45–55 additional short-tailed voles over the lactation period) than it would if it was male-sized (Powell et al, Chapter 11, this volume, present similar data for fishers).

Delayed implantation

Musteloid mating systems, and especially the unique features of their reproductive biology, are a combination of physiological and sociological attributes. Of the former, the enigma of delayed implantation (DI) occurs in 34 species of mustelid (Mead 1989; Sandell 1990), accounting for almost 50% of the 54 carnivore species with DI. Curiously, this reproductive physiology is absent from the procyonids, but tentatively suggested for the red panda (Roberts and Kessler 1979). DI serves to disarticulate the mating and the birthing season, allowing up to an entire year between the two in post-partum breeders, rather than the 30–60 day gestation typical of musteloids. Consequently both stages in the reproductive process can happen at optimal times of the year. This avoids the need to mate during the depths of winter for cold-climate species, which would otherwise be needed to achieve spring parturition dates, also allowing offspring the full summer to mature before harsher winter conditions return (Mead 1993).

Among those mustelids with DI, some species (American mink, *Neovison vison*, and striped skunk, *Mephitis mephitis*) have variable gestation periods involving only a few days of delayed implantation (short interval), occurring only if the females are mated early in the season. Other mustelids have obligate DI (long interval) (western spotted skunk [*Spilogale gracilis*], many badgers [*Taxidea taxus, Meles* spp.], *Martes* spp., fisher [*Pekania pennanti*], wolverine, etc.), lasting several months (Mead 1981). Curious pairings of ecologically and phylogenetically similar mustelids with and without DI are apparent; the North American river otter (*Lontra canadensis*, with DI) and Eurasian river otter (*Lutra lutra*, no DI); the stoat (*Mustela erminea*, DI) and weasel (*M. nivalis*, no DI); and the western (*Spilogale gracilis*, DI) and eastern (*S. putorius*, no DI) spotted skunk (see Thom et al. 2004a).

The patchy expression of this trait has been investigated in several meta-analyses. Lindenfors et al. (2003) propose body-size as a driver of DI: for example, weasels (no DI) versus larger stoats (with DI)—Sandell (1984) arguing that this is in response to a high selection pressure for early breeding in the stoat and strong selection for a high potential population growth rate in the weasel. Indeed, adult male stoats mate with neonates when they are only three weeks old, to ensure fertilization, whereas with direct implantation weasels are the only mustelid/-oid able to have two litters per year. Mead (1981), however, refutes a size-based explanation, reporting that, overall, body mass of female mustelids does not differ between species with and without DI. Instead, Mead postulates that DI correlates with low population density and large individual home range size (scaled allometrically); features often associated with mustelids living in seasonally unproductive environments (i.e. seasonality, temperature, snow, latitude,

and primary productivity were all inter-correlated predictors of the trait). For example, the American marten (*Martes americana*) typifies a low density, diffuse, polygynous, superfecund species, with DI.

Induced ovulation

In these low-density, diffuse populations finding mates can be challenging, which risks that a female might ovulate wastefully, without finding a male to fertilize her. It appears that all mustelids in which the trait has been investigated have induced ovulation (IO) (Amstislavsky and Ternovskaya 2000). In the orgy of high-density badger mating, IO is likely exploited as a mechanism for extending mate choice (Macdonald et al. 2015b). There is, however, an attendant risk to females. As author CN, working with Andrew Byrne, explains in Chapter 9 (this volume), it is well established in domestic ferrets (domesticated polecats, *Mustela furo*) that if females (jills) fail to mate, prolonged high levels of oestrogens during the un-terminated oestrus can cause sickness and death. These high oestrogen levels also cause the cervix to remain partially dilated, allowing uterine bacterial infections that can develop into pyometra and fatal toxaemia. In captive ferrets, this cascade can be prevented by the 'jill jab'—a progesterone (proligesterone) injection that terminates oestrus (or by mating with a vasectomized male, assuming breeding is not an option). The literature is sparse on how failure to mate can impact wild mustelids—where objectively, unrestrained by captivity, females will seek out mates whenever possible. Nonetheless, wild polecats and black-footed ferrets are close genetic relatives to domestic ferrets; Johnson et al. (1999) report pyometra in a Siberian polecat (*Mustela eversmanii*)—indeed all un-mated female mustelids could be at risk.

Whether procyonids exhibit IO is debated, certainly Kaufmann (1982) reports IO in raccoons—or at least that females deprived of males did not ovulate (although visual, auditory, and olfactory interaction with males—without mating—did cause ovulation), whereas Zeveloff (2002) reports spontaneous ovulation; indeed pseudo-pregnancy has been recorded in some un-mated raccoons. Several male raccoons can mate with a single female (and males will mate several females) and multiple paternity occurs amongst litters (of eight raccoon litters examined by Nielsen and Nielsen 2007, more than 88% were sired by multiple males). Similarly, Hirsch and Gompper (Chapter 28, this volume) describe how male coatis congregate with female bands in the mating season, with several males mating each female (often with fierce competition between males), potentially to stimulate IO. Unfertilized raccoons, or those losing their litters soon after parturition, may have a second oestrus around four months later in the year. Red pandas do, however, appear to be induced ovulators (Roberts and Kessler 1979; Macdonald et al. 2005).

Ecological influences on mating systems

These physiological reproductive adaptations are interwoven with the basic musteloid mating format that we described earlier (see Powell 1979a), with myriad variations, associated with body-size, ecotype, phylogeny, and social system. For example, skunks (Mephitidae) largely follow this basic pattern (Verts 1967; Hass and Dragoo, Chapter 24, this volume), where males alter their territory configurations in the mating season to encounter females, while maintaining smaller territories through the rest of the year; similar to what we have detailed for Japanese badgers (Kaneko et al. 2014).

Circumstances in which food resources and diet drive home range overlap have implications for encountering mates, especially when home range configurations are fluid over time. For example, European polecat (*Mustela putorius*) females occasionally have overlapping home ranges when carrion plays a significant role in their otherwise carnivorous diet (Lodé 1996); similarly, stone marten (*Martes foina*) females can attain high densities, when foraging extensively on anthropogenic food sources, such as cultivated fruits in gardens, implying range overlap (Hisano et al. 2016). In a study of stone marten mating behaviour, Genovesi et al. (1997) noted a case where males displayed limited seasonal variation in the area encompassed by their exclusive territories. This was despite male density being almost equivalent to female density, which would usually favour a roaming strategy (Sandell 1989), where the males of some musteloid species abandon their territories completely in the mating season (Yamaguchi et al. 2006). Furthermore, Genovesi et al. observed instances where males continued to associate with the litters they sired as offspring matured, but without direct paternal provisioning; which they termed paternal-investment polygyny. They posited that mating pair familiarity might reduce the incidence of intraspecific aggression, and that male paternal investment might benefit offspring survival through food provisioning, defence against conspecifics and other predators, and the training of young. In this volume, Jeff Copeland

and colleagues (Chapter 18) describe a similar mating system for wolverines. Male wolverines have almost exclusive intra-sexual territories that encompass 1–4 females and wolverine offspring were rarely sired by individuals other than the established resident male.

Transient, non-territory holding males pose a risk, however, occasionally stealing copulations. Copeland et al. report that males, to protect their reproductive investment, linger in the vicinity of females' natal dens, and may even associate directly with their offspring.

Box 6.1 Contrasting mating systems: Mink versus badgers

The different ways in which musteloid mating strategies have evolved are neatly illustrated by contrasting group-living European badgers and solitary American mink from our own studies (see Macdonald et al. 2015a, b). Shared and divergent traits evident between these species provide a framework with which the broader mating systems of musteloids can be explored.

Both species are polygynandrous and promiscuous, with multiple males mating with multiple females. Earlier we also noted that sexual size dimorphism is lower among larger musteloid species. As a result, males of the larger musteloids are often not sufficiently dominant over females to coerce them, leading to, for example, female European badgers being able to reject the advances of male badgers. In a free-choice experiment, Thom et al. (2004b) showed that although female mink were mated multiply, they were able to resist copulations, and inferred that polyandry is driven by female behaviour rather than male coercion (Macdonald et al. 2015b).

The advantage of promiscuity to males is clear; the more females they fertilize, the more progeny they will produce. But for females, promiscuity has more nuanced benefits. While males can sire multiple litters per breeding cycle, females are restricted to the litter they conceive, and so making the best choice among available males becomes important. In both badgers and mink, this choice is exercised through extended oestrus, where the female can (and may have to) mate multiple times in order to induce ovulation (IO) (Milligan 1982; Larivière and Ferguson 2003). To what extent the female can control ovulation physiologically is unknown, although it seems likely that females use inferior early matings to stimulate ova release. A female can then mate with the best partner available to her at just the critical moment. The male counter-strategy to such manipulative match-making is generally through sperm competition (Clutton-Brock and Parker 1992; Yamaguchi et al. 2006), where not just the semen of the final pre-ovulation mating partner may be in the swimming race to conception, but those of previous partners too (although sperm competition has not been fully substantiated in either badgers or mink).

But additional strategic refinements have also evolved in both badgers and mink to extend the gene-pool of potential fathers. Specifically, there are mechanisms that allow females to choose more than one father for their offspring per reproductive cycle, enabling them literally not to put all their eggs in one basket. One such physiological device is superfecundation (Yamaguchi et al. 2006); the release of two or more ova from the same oestrous cycle. Of course, if the same male fertilizes both ovulations, it is difficult in retrospect to diagnose the gynaecology involved, although in both badgers and mink, genetics expose (see below) hetero-paternal superfecundation, that is, dual paternity litters. A further device is superfoetation (Yamaguchi et al. 2006), where a second oestrous cycle can occur during the gestation of the first round of embryos, also resulting in multiple-paternity within litters—a process perfected in the mustelids through delayed implantation.

In badgers, oestrus and mating occur postpartum, beginning in February; however, embryonic development is suspended *in utero* at the blastocyst stage, prior to implantation and placenta formation. Day-length, modified by body-fat levels (Woodroffe 1995), ultimately trigger implantation around the shortest day of the year (Macdonald et al. 2015b). During this delayed implantation badgers continue their libidinous and protracted mating activity; however the offspring conceived through this polygynandry are not restricted to an individual's home group: around 48% of cubs have an extra-group father (Annavi et al. 2014a). In other carnivores, a neonate born to a non-group-member father would likely be killed (e.g. lions *Panthera leo*—Packer and Pusey 1983). Badgers are, however, so promiscuous—including mixed paternity within litters to include both extra-group and within-group offspring (Dugdale et al. 2007)—that all males are likely to have mated with all the females they meet regularly. As a result, males are likely so confused that they cannot rule out that they could be father to her cubs, reducing the tendency for males to commit infanticide (Agrell et al. 1998; Palombit 2015), which might otherwise stymie population dynamics. Consequently, the costs and benefits of bearing 'within-group'
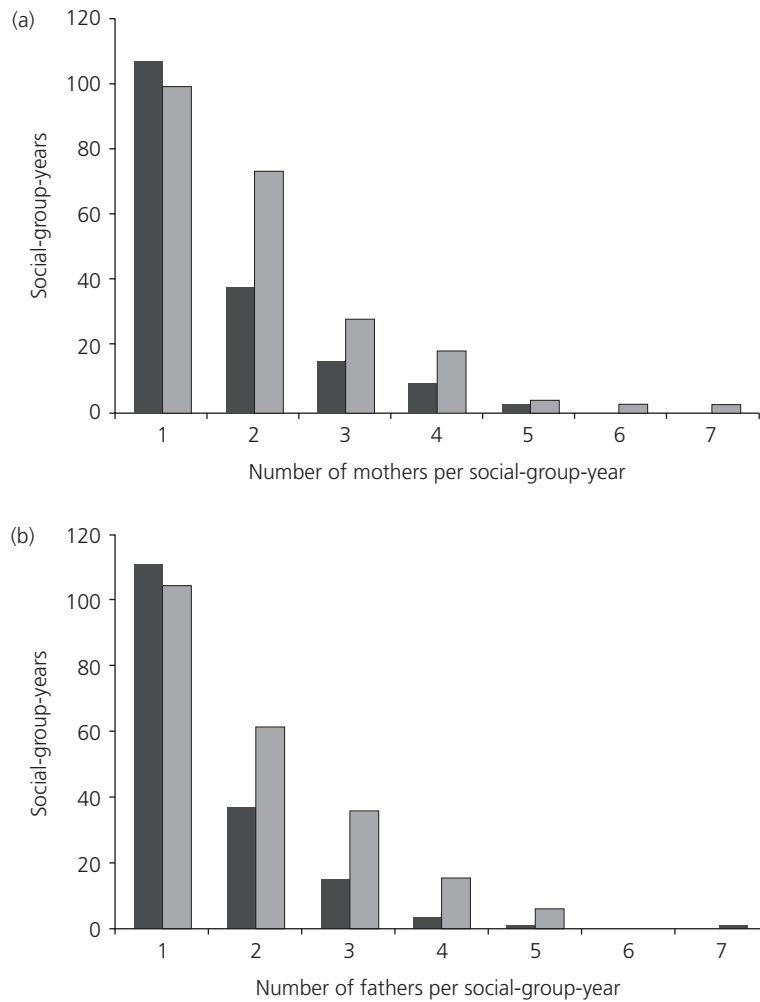
Box 6.1 *Continued*

versus 'extra-group' offspring turn out to be a subtle inter-play of social and genetic factors; certainly it's not as simple as seeking exotic genes (Annavi et al. 2014a, b; subm. Macdonald et al. 2015b; Sin et al. 2016).

Social system, population densities, and life-histories are pertinent here. In natural North American habitats mink are quite dispersed (e.g. Bowman et al. 2007), and females exhibit short interval DI, supplemented by superfecundation, allowing them to prospect for more and better males—but

only over a sustainable period that still allows females to give birth in the same spring as conception. Despite the abundance of badgers in the UK, in other continental European regions these too are often a diffuse, low density species (Johnson et al. 2000). Again, DI combined with superfecundation permits an extended period of mate selection, while, simultaneously, long interval DI effectively allows badgers to give birth before they breed in any single year. In badgers decoupling conception from gestation also ensures that cubs

Figure 6.6 Average number of (a) mothers and (b) fathers per group assigned offspring per year. From Dugdale et al. (2007).

Box 6.1 *Continued*

are born at the optimal time of the year (mid-Feb with a *c*.56 day gestation after implantation) to permit weaning in May when earthworms and other food sources are usually abundant (and thus, as described in Newman et al., Chapter 21, this volume, dry springs can cause severe cub mortality). This gives cubs the full summer and autumn to feed, develop and fatten up, ahead of their first winter (when under-sized cubs die; Macdonald and Newman 2002). For a conventional, direct mating system to accommodate a mid-February birth date, mating would have to take place in mid–late December. This would be highly unsuitable, because during cold, unproductive winter nights badgers use torpor to conserve energy (Noonan et al. 2014)—completely incompatible with courtship. Indeed, in colder parts of the range of *Meles* spp., and during colder periods of the evolution of these species, this torpidity extends to semi-hibernation (Zhou et al., Chapter 13, this volume). Group-living typically involves the

reproductive suppression of subordinate females, at the hormonal level, inhibiting oestrus (Creel and Creel 1991). This is not the case in badgers, where several cohabiting females may produce cubs successfully in the same set in the same year. Nevertheless, in Wytham, genetic pedigree exposes that although most females mate, only about 30% of females bear young each year, although up to seven females (and males) have been found to breed per group (Dugdale et al. 2008; Figure 6.6).

It is enlightening, therefore, that, despite group-living, badgers effectively retain a mating strategy functionally and physiologically very similar to that of solitary mink, and so follow a basic strategy that is undertaken by many cohabiting individuals, rather than a special case. Each badger continues to act as an independent agent, unified into the semblance of a group primarily through philopatry and RDH-driven cohabitation.

Effects of diet and food dispersion on mating systems

The exploitation of different trophic resources also affects social and mating systems. When extensive and often permanent home range overlap occurs this has mating system implications; a situation characterizing several otter species. Asian small-clawed and smooth-coated otters are unusual among musteloids because they tend to form monogamous pairs. Sea otters have an elaborate mating system; they are polygynous with substantial sexual dimorphism, and tend not to breed successfully until six to seven years old. According to Jim Estes and colleagues (Chapter 23, this volume), oestrus, impregnation, and gestation appears to be 'hard wired', where a new breeding cycle is triggered immediately after a female separates from her preceding pup, regardless of the time or cause. Consequently, there is no firm breeding season, and females give birth throughout the year. Furthermore, mothers in poor condition often abandon their pups almost immediately, before they invest in the energy-expensive phase of lactation and weaning, and begin another oestrous cycle (Staedler 2011). Breeding males cease to mix with other otters in their raft (a congregation, but not a social group) and begin to patrol and defend a territory through display and vocalization, rarely fighting. Adult females move freely between

these male 'leks' (where populations generally have a substantial female sex bias). Meanwhile, non-territory-holding males congregate into cliques, and may swim through female rafts trying to steal mating opportunities. During mating, the male mounts the females by gripping his teeth onto her nose and wrapping his forelegs around her chest. Mating lasts between 15 and 30 minutes and is intense, likely to induce ovulation. Developing blastocytes then undergo a variable length of delayed implantation (Sinha et al. 1966), but births occur year-round, with peaks between May and June in northern populations and between January and March in southern populations (Love 1992). Typically only a single highly altricial pup is born at sea, and only one will survive amongst twins. In northern ocean populations, females tend to reproduce every second year.

One of the most unusual musteloid mating systems is that of giant otters (Groenendijk et al., Chapter 22, this volume), where reproductive suppression leads to only the dominant pair breeding. Other group members achieve inclusive fitness by helping to provision pups with fish and assisting in their care. Comparing this most social of otters against the most 'social' of the terrestrial mustelids, the plurally breeding European badger, we thus see a dichotomy, because most badgers in a group mate and several can be successful (Dugdale et al. 2008; see Figure 6.6). These individually motivated mating patterns of badgers appear to enact

a standard mustelid mating system squeezed into a spatial-group scenario, whereas the mating system of giant otters shows more complete integration into their altruistic society.

Procyonid mating systems

Thus far we have focused on the mustelids. With a more generally tropical distribution, the Procyonidae do not have DI, and evidence for OI is equivocal, thus their mating systems seem to be governed more by sociological, than physiological, traits.

The mating system of raccoons seems quite variable. In low productivity areas, both sexes are solitary most of the time, with exclusive intra-sex ranges (Zeveloff 2002). With greater environmental productivity, 'fission–fusion societies' emerge, with females exhibiting various extents of range overlap. Similarly, unrelated males sometimes form 'gangs' of up to four individuals to ward off invading males during the breeding season. Subordinate males, however, may still get a mating opportunity in populations with a female bias. Male raccoons can be aggressive to unrelated kits, and so females tend to avoid males until their litter matures (Hohmann et al. 2001).

This infanticide risk, posed by males, goes a step further in coatis (see Wolff and Macdonald 2004; Hirsch and Gompper, Chapter 28, this volume). We have discussed how females form permanent bands to protect their offspring from marauding males. Within these bands oestrus is synchronized. During the mating season a male will be accepted into the band, leading to polygynous mating. As a consequence, there is strong reproductive skew concerning which males get to breed. Pregnant female coatis leave the band temporarily to give birth, to hide away from potential predators. They rejoin their band when their kits are around six weeks old—notably, these mobile scansorial kits develop much more precociously than fossorial badger cubs. Males disperse from the natal band as they reach sexual maturity. Coati bands thus comprise multiple breeding females with overlapping foraging ranges, but without reproductive suppression.

Moving deeper into tropical latitudes, kinkajou mating systems are quite peculiar, with often two males, one dominant, the other subordinate, and a single female comprising a breeding unit (Brooks and Kays, Chapter 26, this volume). In addition to mating with their own-group female, the dominant male will also attempt to mate with neighbouring females, as well as any other females living on the periphery of its home territory (Kays 2003). Occasionally the subordinate male may get to mate with his group's female (Kays and Gittleman 2001; Kays 2003), although genetic analysis of paternity indicates that subordinates sire few offspring (Kays et al. 2000). Nevertheless, this leads to polygamy with weak polyandry. Females are in oestrus for up to 17 days, roughly synchronized into a localized breeding season that is probably tied to local fruit production in each geographic region (Kays and Gittleman 2001). Curiously, the subordinate male seems to aggravate and occasionally fight with the dominant male during courtship—suggesting that while the subordinate helps to defend a larger territory than a single male could alone (Kays and Gittleman 2001) its role during the breeding season is not necessarily to support the dominant male. Litters comprise one, rarely two, pups, where the female provides a high degree of investment into this single offspring; males provide no care, but neither do they pose a threat to young. Because kinkajous eat mostly fruit, with a low calorific value, gestation and lactation place severe stresses on female energy budgets, limiting mothers to predominantly singleton litters—even then, she will feed voraciously while providing maternal care (Kays 2003). Central American, mostly fruit-dependent cacomistles similarly have just one young per year, but have a more conventional solitary mating system (Poglayen-Neuwall and Toweill 1988).

Fossoriality and group-living

Building on the RDH mechanism, we have recently (see Noonan et al. 2015a) conceptualized and exemplified how traits linked to 'fossoriality' (i.e. the use of underground space), cultivate the congregation of conspecifics; a concept we termed the Fossorial Benefits Hypothesis. Explicitly, we propose that if the benefits provided by fossorial dens result in a situation where the offspring survival probability associated with philopatry is greater than with dispersal, natal philopatry may leverage group-living. From meta-analysis, we found that carnivore species utilizing subterranean dens are roughly 2.5 times more likely to form social groups than those that do not. Relevant here is that extant musteloids are the most fossorial carnivore lineage, adding to the importance of this mechanism within this super-family. Musteloids are also relatively small among the Carnivora, where the cost associated with burrow construction scale with body mass (M) according to $\alpha M^{\circ.54}$ (Vleck 1981), and the force an animal can exert scales according to $\alpha M^{\circ.25}$ (Biewener 2005).

Actual burrow size also scales allometrically ($\alpha M^{0.33}$, see Vleck 1981) setting an upper limit on burrow size imposed by structural stability (White 2005). As a consequence, canids tend to quickly outgrow natal dens (Noonan et al. 2015a), while the felids, procyonids, and viverrids evolved along trajectories incompatible with digging (Macdonald 1992; Andersson 2004).

Most significant, however, is neonate altriciality, where musteloid offspring are particularly altricial at birth, and slow to develop, thus many species excavate underground natal dens to provide warmth and protection (Noonan et al. 2015a). The substantial neonate survival benefits of fossorial dens (Kaneko et al. 2010), favour philopatry until opposing forces drive maturing offspring to disperse (Macdonald 1983; Noonan et al. 2015a). This results in varying extents of delayed dispersal. Species dispersing immediately after weaning (e.g. Sheffield and King 1994) are typically solitary. Where offspring remain philopatric until sexual maturity (e.g. Kaneko et al. 2014), temporary maternal-offspring groups arise. If these groups retain breeding adults (Woodroffe et al. 1995), stable adult groups result.

The ability to cohabit within dens into adulthood is, however, also a function of resource abundance and dispersion. As discussed, diet type and resource dispersion play a central role in determining individuals' ability to share territories. Strictly carnivorous musteloids tend to disperse from natal dens as they mature (Noonan et al. 2015a)—for example, American badgers (*Taxidea taxus*)—because territories cannot sustain growing energetic demands of juvenile groups. In contrast, for those musteloids that consume a diet where food resources have a dispersion able to support adult groups, typified by omnivory/insectivory (*sensu* Macdonald, 1983)—for example, European badgers (Macdonald et al. 2008)—dispersal may be delayed or obviated entirely.

Derived benefits and implications of group-living in musteloids

When canid and felid species form multi-adult groups they typically exhibit collaborative behaviour, notably cooperative hunting of large prey and allo-parental care (Macdonald et al. 2004a; Macdonald et al. 2010b). When societies are RDH-based (Macdonald and Johnson 2015), however, group-living is primarily facilitated by ecological factors rather than sociological benefits (although secondary sociological benefits often follow); rather these are 'groups of convenience'

where alternative socio-spatial geometries would be less effective. The fact that our summary of cooperative behaviour amongst musteloids is populated by fewer examples than documented in the equivalent chapters for canids and felids (Macdonald et al. 2004a; Macdonald et al. 2010b) may not solely be due to observer bias, but rather may reflect that several instances of group-living amongst musteloids appear to develop within an RDH framework rather than a cooperative one.

In terms of intensity of social interactions, it is only really the coatis (Chapter 28) and some otter species, notably giant otters (Chapter 22), that interact with the level of communal enthusiasm seen amongst African wild dogs (*Lycaon pictus*, Creel and Creel 2002), bush dogs (*Speothos venaticus*, Macdonald 1996) and meerkats (*Suricatta suricatta*, Doolan and Macdonald 1999) and others among the exuberantly sociable Carnivora (Creel and Macdonald 1995; Macdonald 1992). Spatial groups arising purely from the RDH ostensibly need not exhibit any direct group-living benefits, beyond achieving adequate food security. Nevertheless, there are still behavioural consequences (costs and advantages) for musteloids accommodating conspecifics in close proximity.

Communication

Living in groups inevitably brings a host of challenges for communication. Christina Buesching and Ted Stankowich (Chapter 5, this volume) discuss modes of communication and behavioural contexts, explaining how the complexity and subtlety of signals tend to increase with gregariousness. All musteloids make defensive hisses and growls, and use vocalizations as maternal-offspring appeasement or contact calls, but more intricate repertoires are the domain of group-living species. Social otters, especially giant otter, African clawless and Asian small-clawed otter groups are very vocal, as are bands of coatis; kinkajous grunt and squeak to each other, but are most infamous for their eerie scream, where their Spanish folk-name '*la llorona*' translates as 'the crying woman'.

As we postulated above, group-living in European badger groups seems much less thoroughly evolved than other gregarious musteloids, arising as the product of recent agrarian practices enhancing their food supply (Macdonald et al. 2015b). Predictably then, although badgers do have distinct calls (Wong et al. 1999), they are surprisingly quiet animals, using soft grumbles for appeasement, but capable of fierce snarls if challenged. Instead, badgers communicate with scent, having evolved unique subcaudal glands that encode

individual-specific as well as group information. In this olfactory context, all musteloids use the scent cues in their urine and faeces to mark their dens and territories (Brown and Macdonald 1985), both through a saturation of scent marks and by focussing marking on their range periphery, or 'border' (Buesching and Jordan in press). Group-living species take this behaviour a step further, and tend to co-ordinate their marking to demarcate their group-specific territory (Buesching et al. 2016a).

Visual signals are relatively few amongst musteloids, largely due to the majority of species being nocturnal. While the aposematic coloration of skunks is conspicuous, this serves mostly to convey their noxious capability to other species (Stankowich et al. 2011; Buesching and Stankowich, Chapter 5, this volume). Only the throat patches seen in some otter and marten species seem to play a role in social recognition (Groenendijk et al., Chapter 22, this volume).

Cooperative hunting

Even when high prey patch richness causes individuals to aggregate, there is scant evidence of musteloids hunting collaboratively—largely because they can despatch their small prey without assistance. Wroughton (1917) equates groups of martens scavenging on the same carcass with group-hunting (which he termed 'martelism'), although in the absence of firm evidence supporting this contention, Newman et al. (2011) only ascribe martens with the ability to tolerate close mutual contact at rich feeding sites. There is similar speculation that the South American grison (*Galictis cuja*) might hunt cooperatively (Diuk-Wasser and Cassini 1998). Tayras (*Eira barbara*) forage in pairs or family groups (Ferrari 2009), and coatis appear to forage more efficiently for lizards in groups (Gompper 1996). Groups of smoothed-coated otters herd fish into the shallows—indeed, fishermen train them to herd fish into nets (Feeroz et al. 2011). The strongest candidate, though, for cooperative hunting amongst musteloids is the giant otter—tight groups of otters engage in leaping dives, called porpoising, and surface with fish after fish. Nevertheless, observations and interpretations are few (Carter and Rosas 1997; Rosas et al. 1999) and none quantify any per capita energetic gain when hunting together rather than separately (but see Groenendijk et al., Chapter 22, this volume).

Mutualisms across the taxonomic divide are also worthy of mention. In 1785 Sparrman reported hearsay that honeyguides (*Indicator indicator*; a passerine-like bird) work with honey badgers, although many consider this a fallacy. Honey badgers have, however, been reported to hunt commensally with the pale chanting-goshawk (*Melierax canorus*) and black-backed jackal (*Canis mesomelas*), although without significant costs or benefits (Begg 2001). While coyotes enjoy higher capture rates while hunting ground squirrels in company with American badger (Minta et al. 1992), and the badgers probably save energy too, Lehner (1981) proposed that coyote–badger associations are phoretic (accidental and non-obligatory) rather than a form of social symbiosis. Similarly, pied kingfishers (*Ceryle rudis*) are said to be commensal on foraging African clawless otter, but the favour is not returned (Ruggiero 1998).

Allo-parental care

Cooperative breeding is rare among musteloids although, once more, giant otters stand as a remarkable exception. In Manu National Park, Peru, non-breeding adults of both sexes provision the pups born to their group's breeding pair with fish (Groenendijk et al. 2015b; Groenendijk et al., Chapter 22, this volume). The greater the number of these non-breeding helpers, the greater the number of pups that survive to become juveniles. Furthermore, larger groups hold larger territories, and pups produced on these larger territories are more likely to disperse and breed successfully. Interestingly too, this society not only cares for the young, but also for the old, with Davenport (2010) reporting multiple forms of assistance given to the declining group matriarch.

The unusual social system of kinkajous also implies an extent of allo-parental care (Brooks and Kays, Chapter 26, this volume). In addition to the resident female and her two adult male consorts, cubs and philopatric sub-adults also remain within the family group (Kays and Gittleman 2001). Groups are competitive, and thus the presence of extended family offers vulnerable offspring protection. Furthermore, males have been observed engaging in grooming and even playing with the young. Copeland et al. (Chapter 18, this volume) report similar nebulous paternal benefits in wolverines, where the father of litters will spend time at the natal den (sometimes split between more than one family) and will interact with his offspring, perhaps protectively, even once they are independent.

Despite thousands of hours of observation, there is only fragmentary evidence of allo-maternal care in European badger groups. In video observations of 23 suckling events of 24 cubs from three groups, Dugdale et al. (2010) report two mothers that may have been

nursing a larger number of cubs than their own assigned litters. Notably too, it is easy to mistake cubs engaging in scent theft, to anoint themselves with subcaudal secretion by ducking under the belly of an adult (Fell et al. 2006), with suckling—only this scent acquisition behaviour persists long after weaning. Additionally, Dugdale et al. (2010) report 186 instances when adults carried cubs (10% by males), but these may have been their own offspring, and the functional significance of this translocation was not clear. In short, if allo-maternal behaviour occurs in badgers it seems at best rudimentary and the exception rather than the rule. Eighteen years of genetic pedigree (Dugdale et al. 2010) revealed neither short-term (litter size; maternal survival to the following year) nor long-term (offspring breeding probability; offspring lifetime breeding success) fitness benefits occurring more with either within-group mothers or other group members—indeed, the number of other group members within a social-group-year had a negative relationship with both the probability of a cub breeding and the lifetime breeding success of a cub.

Coatis take this a step further, and bands of females actually break-up around their synchronized parturition dates (Hirsch and Gompper, Chapter 28, this volume) and females give birth alone—a strategy believed to be linked to lone mothers being better able to evade the detection of their natal nests by predators, rather than due to threat of intraspecific infanticide.

Interestingly, linked perhaps to a lack of reliance on visual senses in musteloids, Buesching and Stankowich (Chapter 5, this volume) highlight that, unlike most other Carnivore families, young musteloids, especially mustelids, lack the distinct neotenic 'kindchenschema' that would usually solicit care-giving; those features that cause people to find kittens and puppies 'cute' (and while baby kinkajous look cute, this only reflects adult attributes). Again, this likely ties into the rapid independence of non-group-living musteloids, and the tendency for delayed dispersal to be associated with group formation. While maternal, parental, and even alloparental care feature amongst some lutrine and procyonid group-living species, badgers again stand out with steadfast indifference toward cubs (Fell et al. 2006).

Vigilance and defensive behaviours

Predation is an important factor in the evolution of sociality among animals. Musteloids are generally quite small, and often must compete with larger, sympatric, intra-guild competitors. Nevertheless, musteloids tend to be fierce, and hunters and trappers have learnt not to cross wolverines and honey badgers, where conspicuous aposematic facial masks advertise their disproportionate ferocity (Newman et al. 2005; see also Buesching and Stankowich, Chapter 5, this volume). Indeed skunks (including old world stink badgers—see Zhou et al., Chapter 13, this volume) take this to an extreme, where their boldly dichromatic pelage advertises the noxiousness of their anal gland discharge, capable of repelling any potential sympatric predator (Stankowich et al. 2011).

The alternative to actual or professed fierceness in the light of a larger adversary is to avoid conflict in the first instance. The musteloids thus tend to invest heavily in individual vigilance. In group-living species, the burden of vigilance can be shared, as seen in smooth-coated otters (van Helvoort et al. 1996) and colonial sea otters when resting on land (Maldini et al. 2012). Amongst musteloids, coatis exemplify perhaps the most extreme example of cooperative defensive behaviours, including foraging with the juveniles in the centre of the group, sharing vigilance, alarm calling, and mobbing and attacking predators; which suggests that predation has shaped their society (Di Blanco and Hirsch 2006). Similarly, Burger and Gochfeld (1992) found that coatis drinking from dangerously exposed waterholes risked more drinking bouts when in larger groups, and that members of larger groups also stayed at the waterhole for longer and were individually less vigilant than members of smaller groups. Hass and Valenzuela (2002), studying white-nosed coatis at sites where jaguars *Panthera onca* and pumas accounted for more than 50% of adult mortality, found predation rates were significantly higher on solo coatis than on those in groups, and decreased with group size.

Raccoons also live in a landscape of fear amongst larger North American predators. This has been demonstrated experimentally by Suraci et al. (2016), who found that playing large predator vocalizations through loudspeakers could substantially disrupt normal raccoon foraging behaviour, with cascades through the food-webs of their prey. In a similar experimental trial, we observed that badgers in the UK exhibit increased vigilance, and reduced foraging on artificially provisioned sites, when the sounds of bears and dogs (but not wolves) were broadcast (Clinchy et al. 2016). Crucially, however, the sound that caused badgers greatest anxiety was that of people talking, suggesting that fear of humans is also cause for concern amongst carnivores in close human contact, prone to persecution (Clinchy et al. 2016).

Although cooperative defence is commonplace for mammalian societies in general (Armitage 1987), and carnivores in particular, there is little evidence for co-operative defence amongst musteloids. Again, this is likely tied to the majority of group-living species foraging alone, and that they are often capable of mounting a substantial counter-attack without assistance. There are, however a few examples of group defence: giant otters see off their rivals and marauding caiman (Ribas et al. 2012), and Cape clawless otter groups defend against conspecifics. A plausible, if unproven, suggestion is that large rafts of sea otters may confuse cruising sharks (Garshelis et al. 1986) and orca (Hatfield et al. 1998). Doubtless too, large groups (4–25) of female coatis are empowered to contend not only with threats of having their prime feeding sites usurped by much larger male coatis, but also with predation from jaguars, pumas, and capuchin monkeys *Cebus capucinus* (see Blundell et al. 2002). Similarly male raccoons can benefit from collaborating in territorial defence (Pitt et al. 2008).

Mutual interactions

Even solitary animals regulate some of their behaviour with respect to other individuals, while attempting to remain out of contact (Eisenberg 1966), and so 'solitary' is not contrary to 'social' (see Leyhausen 1964). Sandell (1989) qualifies this distinction with the injunction that 'no collaboration between members in feeding, defence of territory, offspring-rearing, and mating, even in cases where ranges overlap' still constitutes solitary behaviour, even within a socially organized spatial geometry; that is, gregariousness, as seen in sea otters, and to some extent European badgers, does not intrinsically imply sociability. But what of more integrated group-living species? What other collaborations outside of mating and defence become accessible to these?

Allo-grooming characterizes many group-living mammal societies, from primates (Sparks 1967) to impala *Aepyceros melampus* (Hart and Hart 1992). Allo-grooming can serve a variety of functions, involving conflict resolution, reconciliation, and precoital bonding, but arises from the fundamental need for animals to maintain good health and hygiene by removing ectopic parasites—a task where others might reach parts the individual cannot reach themselves (e.g. Tanaka and Takefushi 1993). Indeed, group-living, and den-sharing, can often increase each individual's exposure to parasites and pathogens (e.g. Côté and Poulinb 1995). Being groomed releases beta-endorphin, hence its relaxing appeasement quality (Keverne et al. 1989);

furthermore it is associated with increased serotonin production. Significantly, however, concentrating on allo-grooming is known to distract individuals from predator vigilance (e.g. Cords 1995).

All group-living musteloids allo-groom to some extent, probably as an extension of maternal care, ridding offspring of fleas, lice, and ticks. Despite aquatic lifestyles, otters still carry a variety of ectoparasites in their dense pelage, and so allo-grooming is likely useful as well as socially unifying. Kinkajous and coatis allo-groom in groups; but then again we arrive at the paradoxical European badgers, only just on the cusp of evolving secondary benefits from group-living. Attempting to control predominantly the large badger-specific flea, *Paraceras melis* (known to be a vector of trypanosome blood parasites—Lizundia et al. 2011), badgers groom alone extensively, focusing on the chest and belly (Cox et al. 1999). Allo-grooming requires trust—and badgers tend not to trust each other much. We have found that itchy badgers initiate grooming of a companion, but lose faith and stop if the recipient does not respond in kind—and the duration of this goodwill averages just 1.2 seconds (Macdonald et al. 2000; Stewart and Macdonald 2003). The proportion of grooming time deployed by a badger alone, added to the proportions deployed by a grooming partnership, gives a total such that every zone gets almost equal coverage per unit area (Stewart and Macdonald 2003; Figure 6.7). Once started, cooperative grooming continues until one individual defects, whereupon the other also stops, generally within less than half a second. This approximately tit-for-tat arrangement results in fleas moving between individuals such that all group members end up with an equalized flea load, and thus it pays each badger to contribute to the common good by mutual grooming (Johnson et al. 2004).

Another distinctly badger trait is the excavation of setts (Noonan et al. 2015a). All badgers dig burrows and rest within, but solitary species, such as the American badger (Weir et al., Chapter 19, this volume) and various Asian badgers (Zhou et al., Chapter 13, this volume), including the mephitid stink badgers (along with new world skunks, Hass and Dragoo, Chapter 24, this volume), dig only a simple tunnel usually leading to a single chamber within. Large groups of European badgers require large setts; in our Wytham Woods study population, setts can have more than 50 entrances, stretching 100 m along a bank, and likely involve hundreds of metres of tunnels representing dozens of tonnes of earth moved (Macdonald et al. 2015b). This kind
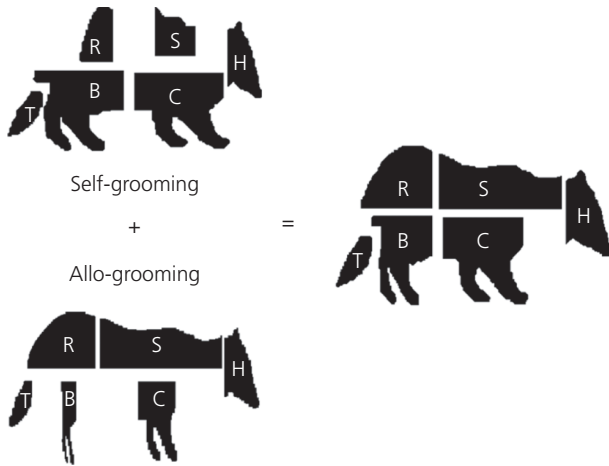
Figure 6.7 A badger can only self-groom certain body areas effectively, and so it solicits allo-grooming of these difficult to reach regions to achieve full body coverage.

of civil engineering would ideally require planning and cooperative effort, but yet again it is not uncommon to see one badger throwing the spoil it digs from the hole it is working on into the path of a badger excavating an opposing hole. Males tend to contribute most to digging the communal setts (Stewart et al. 1999); possibly creating a resource attractive to either retain or attract breeding females.

Conclusions: 'Musteloids can't run, but they can hide'

Boxer Joe Louis famously quipped (Coshocton Tribune, June 9th, 1946), 'he can run but he can't hide' when commenting on his 1946 heavyweight title bout against the lighter, faster Billy Conn (a fight Louis won). Adapting that insight to the strategic divergence that separates the musteloids from other branches of the Carnivore family: Musteloids can't run, but they can hide (and indeed sneak into all manner of crevices and can thereby secure competitive space alongside rival Carnivore families). While felids and canids evolved longer legs and a more fluid gait to run down, stalk, and pounce upon large prey in the proliferating Oligocene grasslands, the musteloids evolved to hunt small rodent prey by either digging them out of (musclimorph) or by following them into (skinnymorph) burrows; subsequently radiating into myriad strategic niches not monopolized by their felid and canid cousins. Thus, through the irresistible force of natural selection, the musteloids 'filled gaps'; as Aristotle observed: '*horror vacui*'—'*Nature Abhors a Vacuum*'.

That musteloids cannot figuratively run with the pack literally rules out the potential for pack hunting strategic benefits. No terrestrial musteloids hunt in packs, and only a few otters hunt collaboratively. Hunting by excavation, burrow pursuit, and stealth offers few opportunities for cooperation and most predatory musteloids tend to be solitary. In contrast, the diversification of musteloids into omnivory, and the extended dietary breadth this entails, creates a reliance upon trophic resources that have dispersion and renewal characteristics that can facilitate group-living. Moreover, the utilization of burrows by many musteloid species facilitates the perpetuation of philopatric natal groups, sometimes into adulthood, congregating together at the group den (Noonan et al. 2015a).

And so, as the other authors contributing to this volume describe in fascinating detail, the procyonids are the brains of the Musteloidea, the otters the beauty, while the brawny badgers exemplify the mentality that all problems inevitably yield to force. They are an ensemble cast of contrarians that do things that bit differently, unified by the major distinction that they are not cats, or dogs; and by the epithet of being 'long, thin, and stinky'.

Acknowledgements