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VERTEBRATE CARNIVORES AND PREDATION IN THE ORIENTAL (INDOMALAYAN) REGION

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***ABSTRACT.* –** Current knowledge about terrestrial vertebrates that kill and eat other terrestrial vertebrates in the Oriental Region is summarised. Carnivory, by this definition, is dominated by snakes, diurnal and nocturnal birds of prey, and members of the order Carnivora, although a wide range of other Oriental vertebrates eat at least some vertebrate prey. The most species-rich lowland forest sites can support at least 45–65 carnivorous vertebrates, which appear to partition prey by type, size, period of activity and spatial distribution, although there are also many species with apparently generalist diets. Most prey types are taken by reptilian, avian and mammalian carnivores, but, except on islands, the largest prey are taken only by the largest mammalian carnivores. Most carnivores take some prey near their own body mass, with the exceptions being mostly specialists on ectotherms or rodents, or omnivores that also consume invertebrates and/or plant foods. Oriental forests support more sympatric mammalian carnivores than anywhere else in the tropics, but fewer snakes and birds than the Neotropics, and apparently fewer sympatric vertebrate carnivores overall. The tiger is the world's largest tropical forest carnivore and the biggest Asian pythons are the largest dryland snakes, but the Region lacks a really large raptor, except in the Philippines. Hunting is the biggest threat to most mammalian carnivores and is often driven by trade, while habitat loss and degradation are the major threats to birds. Introductions from outside the Region are not yet a problem, but translocations of Oriental species to islands may have already had significant impacts. Maintaining intact communities of large carnivores will require protected areas that are much larger and much better protected than most that exist at present. The major research needs are ecological studies of entire carnivore communities at the few sites where these are still intact and conservation-oriented studies of threatened species.

***KEY WORDS.* –** Asia, carnivores, Oriental Region, predation, predators, prey, vertebrates.

CONTENTS

INTRODUCTION

Large carnivores have become flagship species for conservation in many parts of the world. Much of this attention reflects their charismatic image, but there is also some evidence that large carnivores can play an important role as top-down controls on community structure and processes (Gittleman & Gompper, 2005). The role of the much more numerous and diverse smaller carnivores (<15 kg) is less clear, however, even in regions where the ecology of most individual species is well understood (Roemer et al., 2009). Although terrestrial carnivores typically have larger natural species ranges than members of other guilds, their low densities and susceptibility to hunting pressures may make them disproportionately vulnerable to local and, eventually, global extinction (Gittleman et al., 2002). Big endotherm carnivores, in particular, are necessarily rare in intact ecosystems and thus vulnerable to both direct persecution and reductions in prey density. The combination of charisma, vulnerability and potential ecological importance has also made large terrestrial carnivores an attractive target for reintroduction projects.

In contrast, those who live with wild carnivores often hold negative views, because they kill people and their livestock. Others view wild carnivores as sources of meat, skins, and—particularly in Asia—body parts for medicinal use (Corlett, 2007). Not surprisingly, conflicts between these contrasting romantic, ecological, negative, and commercial views of carnivores are a major source of conservation problems. Many species—particularly the larger ones—now occupy tiny proportions of their potential natural ranges and are threatened by direct persecution, prey depletion and habitat destruction.

Successful conservation management is based on ecological knowledge, but, while most carnivores are tropical, most of our knowledge of the role of carnivores comes from species-poor non-tropical communities or from highly degraded tropical environments. Within the tropics, attention has been focused on a few charismatic species, especially the large cats, and very little is known about the numerous smaller taxa. Mammals have received most attention, but they make up less than half the diversity and biomass of vertebrate carnivores and all but the largest mammalian carnivores compete for prey with carnivorous birds and reptiles. The top predators in intact mainland communities are mammals, but birds or reptiles often take the largest prey on islands.

Lack of research is not the only problem in the Oriental Region. Despite its biogeographic coherence, it is fragmented politically and linguistically, and information on carnivores is scattered in numerous publications, many of which are hard to obtain outside their country of publication. The major aim of this review is therefore to summarise what is known about the natural history of carnivores in the Oriental (or Indomalayan) Region. This Region has, except near its margins, a distinct and, at higher taxonomic levels, fairly uniform, flora and fauna. This review is restricted to terrestrial vertebrates that kill and eat other terrestrial vertebrates. Fish and specialised fish-eaters are excluded, as are pure scavengers. It concentrates on the consumption of adult vertebrates, since the sizes of juvenile lizards and snakes overlap with those of insects and their consumption by primarily insectivorous vertebrates requires no special adaptations. Thus restricted, this review deals with a guild of vertebrates that have overlapping diets and some shared adaptations to capturing relatively large and active live prey.

METHODS

The Oriental Region (hereafter "the Region") is defined in the broadest sense to include: Pakistan, India, Nepal and Bhutan below the Himalayan treeline at about 3000 m; Sri Lanka; Bangladesh; Myanmar; China below 3000 m and south of 35°N; Yakushima and the Ryukyu Islands; and Southeast Asia, including Sulawesi, the Lesser Sunda Islands, and the Moluccas (Fig. 1). Pakistan and south-eastern China are transitional to

the Palaearctic Region, while the islands from Sulawesi to the Moluccas are transitional to the Australian Region. I have used this definition in reviews of seed dispersal (Corlett, 1998) and pollination (Corlett, 2004).

A review of predation could, in theory, be ordered by either predator or prey taxa. Although the latter option would have advantages in understanding the role of carnivores in ecosystems, most observations on prey consumption are reported by those studying the predators, so the information on the prey is less detailed, less precise and often less accurate. It is very rarely possible to assess the relative importance of particular predators to prey species from the literature, while the reverse can be done for many of the better-studied predators. Even then, the data quality varies hugely between species. Much of the primary literature on carnivory in the Region reports one or a few observations of the type "X eats Y", where X or Y are often unexpected and atypical.

The constraints of a predatory lifestyle have often resulted in morphological convergence, so traditional classifications, based on morphology, can sometimes give a poor indication of the phylogenetic relationships revealed by recent molecular studies. As far as possible, this account is organised by monophyletic groups, but the positions of some genera are still unclear and, in a few cases, traditional non-monophyletic taxa (e.g. reptiles, lizards) are used for convenience. Information is presented at the generic level or above, unless—as is most often the case with the mammals—enough is known to show significant differences between species. In many carnivorous vertebrates, adult males and females differ considerably in their body weights and probably also, in consequence, in their diets. However, with a very few exceptions, the published dietary records for Oriental taxa are insufficient to investigate this issue, so the sexes are not considered separately here.

Mammal names follow Wilson & Reeder (2005), unless other sources are given, and mean body masses follow Smith et al. (2003), except where an alternative source (or sources) has masses specific to the Oriental Region or where reported adult weights have an exceptionally wide range. Bird names follow Inskipp et al. (1996). The names of other vertebrates follow a variety of recent sources.

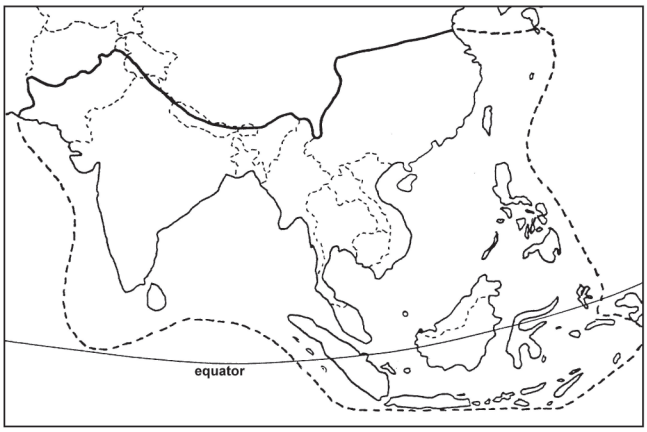

Fig 1. Boundary of the Oriental Region as used in this paper.

AMPHIBIANS

Caecilians feed largely on invertebrates, but occasional consumption of small frogs and lizards has been reported (Daniel, 2002; Presswell et al., 2002; Kupfer et al., 2005). Most adult frogs also feed on invertebrates, but a few large species with disproportionately large heads and wide mouths regularly consume other vertebrates. Most reports in the Region refer to members of four families. *Megophrys nasuta* (Megophryidae) is a highly cryptic ambush predator of the rainforest floor, which is reputed to consume a variety of small vertebrates, including frogs and rodents (Mattison, 1989). Blind snakes, *Ramphotyphlops braminus* and *Typhlops* sp., have been found in the stomach contents of the common Asian toad, *Duttaphrynus melanostictus* (Bufonidae) (Devi, 1991; Hahn, 1976). Several large members of the family Ranidae consume some vertebrates, including the very large (650 g) *Hoplobatrachus tigerinus*, which has been reported to take rats, mice, shrews, birds up to the size of *Pitta brachyura*, snakes <1 m long, lizards, toads and other frogs (Daniel, 2002; Schleich & Kästle, 2002); *H. crassus*, which swallowed an adult tree-frog (*Polypedates maculatus*) (Rodrigo et al., 2004) and *Limnonectes leporinus* (<175 mm), which is reported to eat frogs (Malkmus et al., 2002). An adult of the primarily folivorous *Euphlyctis hexadactylus* in the same family swallowed a 30-cm *Xenochrophis piscator* in 3 minutes (Gupta, 1999). A giant North American ranid, *Lithobates catesbeianus*, is now established on several subtropical Japanese islands and in southern China, and predates native frogs and other small vertebrates (Lever, 2003; Goris & Maeda, 2004; Wang et al., 2008).

REPTILES

Turtles

Turtle diets range from totally herbivorous to totally carnivorous, with some species becoming more herbivorous with age. Almost all records of consumption of vertebrates by free-living Oriental turtles refer to softshell turtles (Trionychidae). Most species seem to be opportunistic omnivores, taking fish and frogs, and occasionally other aquatic vertebrates (Minton, 1966; Schleich & Kästle, 2002; Das, 2010). There is a single bizarre record of several large *Aspideretes gangeticus* killing and eating a nilgai (*Boselaphus tragocamelus*) trapped in a canal in Rajasthan, India (Singh, 2000) and records of the same species attacking a two-year old girl while bathing and killing and consuming a dog (Vyas, 2005).

Lizards

***Varanidae*. –** The Oriental monitors include the two largest living lizards, the Komodo dragon, *Varanus komodoensis* (<3.1 m, 165 kg), on Komodo, nearby islands, and the western tip of Flores, and the widespread water monitor, *V. salvator* (<2.5 m and >20 kg, in some parts of its range), as well as at least 10 smaller species. There are 1–3 species

in almost every habitat in the Region, from deserts to rainforests, swamps and coastal areas (Bennett, 1998). Varanids are powerful, diurnal predators. Most species are apparently extreme generalists, feeding on whatever locally available prey they are able to capture. The predominant prey changes with season, with age, and with locality. The diet has been studied in detail in only a few species, while others are virtually unknown. Some varanids, including the Komodo dragon, produce a complex and potent venom from a gland on the lower jaw, which may compensate for their relatively low bite force (Fry et al., 2009). Varanids are also noted for their relatively complex behaviours and "mammal-like" intelligence, and were described by Sweet & Pianka (2003) as "roughly speaking, dumber than civets and smarter than quolls".

In other ways too, adult *V. komodoensis* behave more like large mammalian predators than like other reptiles (Auffenberg, 1981). Large body size reduces their dependence on ambient temperature and their recurved, laterally compressed, serrated teeth allow them to cut sections from their prey before swallowing, so maximum prey size is not constrained by their gape. Adults can move up to 10 km a day, with a mean of 1.8 km and, again like many mammals, they scavenge or predate, depending on availability. Hatchlings feed initially on insects and small lizards, before moving on to rodents and birds as they grow larger. Large adults often feed on animals as large as or larger than themselves, using stealth and surprise to get close enough. Large prey species include macaques (*Macaca fascicularis*, including large adults), civets (*Paguma larvata*), feral and domestic dogs, goats, wild boar, deer (*Cervus timorensis*, <120 kg), feral horses, domestic and feral water buffalo (*Bubalis bubalis*, weighing <590 kg), and rarely humans (Auffenberg, 1981). All the largest prey are animals introduced by humans, and it has been speculated that their original prey included pygmy elephants (Diamond, 1987).

There has been no long term study of the second largest species, *V. salvator*, but the adults have been reported feeding on a huge range of prey items: invertebrates, fish, frogs, snakes, lizards, turtles, crocodile eggs and young, birds and their eggs, frogs, lizards, rodents, monkeys and small deer (Gaulke, 1991; Shine et al., 1996; Bennett, 1998; Shine, 1998). The remains of a civet and a leopard cat have been found in the stomachs of commercially harvested individuals, but may have been eaten as carrion (Shine et al., 1996). Even large adults of the widespread *V. bengalensis* (<160 cm) feed largely on invertebrates, but they also eat small mammals (including roosting bats), birds and their eggs, snakes (including cobras), lizards, turtles and their eggs, crocodile eggs, fish, frogs and some carrion (Auffenberg, 1994; Sharma, 1996; Traeholt, 1997; Daniel, 2002; Schleich & Kästle, 2002). Most other Oriental varanids for which some dietary information is available consume a variety of invertebrates and small vertebrates (Bennett, 1998).

Other lizards. – Most reports from the Region of non-varanid lizards taking vertebrate prey refer to *Calotes versicolor* (Agamidae), probably more because it is so common and conspicuous, than because it is particularly carnivorous. Although invertebrates make up the great majority of its diet, reported prey include frogs, skinks, geckos (Sharma, 1991a), *Typhlops* (Devi, 1991), a 25-cm *Lycodon aulicus* (Sharma, 1999), eggs and nestlings (Schleich & Kästle, 2002), and a house sparrow (Paralkar, 1995). In West Pakistan, another robust agamid, *Agama caucasica*, is reported to take small lizards (Minton, 1966) as is *Psammophilus blanfordanus* in the Eastern Ghats (Aruna et al., 1993) and several species in Southeast Asia (Das, 2010). Large species of *Mabuya* skinks have been recorded eating a small frog (Minton, 1966) and *Typhlops* (Devi, 1991), and 8 of 11 skink species studied in the Philippines occasionally ate lizards, mostly geckos (Auffenberg & Auffenberg, 1988). *Gekko gekko* (Gekkonidae) will take small rodents, nestlings, small snakes and other lizards (Mattison, 1989; Schleich & Kästle, 2002; Aowphol et al., 2006) and *Hemidactylus leschenaulti* has been observed preying on a skink, a mouse and another species of gecko (Kannan & Krishnaraj, 1988).

Snakes

Unlike most other predatory vertebrates, all snakes swallow their prey whole. The maximum prey size is therefore set by the size of the mouth—specifically, the area available for food passage through the buccal cavity—although in most advanced snakes the left and right lower jaws are connected by an elastic ligament which allows them to separate when engulfing large prey. Ontogenetic changes in diet are the rule in snakes because size has such a large influence on the ability of an animal to capture, subdue and swallow prey.

Uropeltidae. – The uropeltids are burrowing snakes of southern India and Sri Lanka, which lack the elaborate adaptations to increase gape found in more derived snakes. Most species appear to specialise on eating earthworms, but the largest, *Pseudotyphlops philippinus*, is reputed to also eat burrowing frogs (Deriniyagala, 1955 in De Silva, 1990).

Cylindrophiidae. – The Oriental pipe snakes, *Cylindrophis*, are nocturnal burrowing snakes that kill by constriction (Cundall, 1995). *Cylindrophis rufus* (<90 cm) is widespread in wet areas of lowland Southeast Asia and feeds on eels, caecilians, snakes, lizards, nestling mammals and invertebrates (David & Vogel, 1996; Zhao et al., 1998; Stuebing & Inger, 1999). This species has a feeding mechanism intermediate between that of lizards and more derived snakes, which probably restricts it to prey of relatively small diameter (Cundall, 1995). *Cylindrophis maculatus*, in Sri Lanka, is said to prey mostly on other snakes (De Silva, 1990).

Xenopeltidae. – The semi-fossorial *Xenopeltis unicolor* is found throughout Southeast Asia in wet places. Up to 120 cm long, it kills by constriction. Young individuals have hinged teeth, which may be an adaptation to eating shiny, hard-bodied skinks (Savitzky, 1981), although this species is also reported to take other lizards, frogs, snakes, small mammals and possibly ground-nesting birds (David & Vogel, 1996; Stuebing & Inger, 1999). *Xenopeltis hainanensis* is reported to feed on earthworms and frogs (Zhao et al., 1998).

***Pythonidae*. –** Pythons are found throughout the Region, in almost all habitats from rainforest to agricultural and urban areas. They are not only the largest Oriental snakes but are also among the largest Oriental predators. A big python has the body weight of a leopard and can capture and ingest all but the largest of leopard prey species. Where the big cats and the dhole have been eliminated, as in most of the Region, fully-grown pythons are the only predators capable of killing medium-sized vertebrates. Pythons kill by constriction.

The largest python species, and probably the longest snake in the world, is *Broghammerus* (*Python*) *reticulatus*, which can attain 10 m (>100 kg?), although individuals longer than 7 m appear to be very rare. Females grow much larger than males (maxima of 75 vs. 20 kg, 7 vs. 5 m: Shine et al., 1998a). This species is common in all habitats in Southeast Asia, including small islands. It feeds largely on warm-blooded vertebrates, although monitor lizards are also taken (Auliya & Abel, 2000). Most prey is taken by ambush at night on the ground, but pythons also hunt in trees. Fifteen species of prey were identified from a sample of 1070 pythons in southern Sumatra, including 185 rats (3 spp.), 4 mouse deer (*Tragulus* spp.), 1 civet (*Arctogalidia trivirgata*), 2 porcupines (*Hystrix brachyura*), 2 macaques (*Macaca fascicularis*), 12 leaf monkeys (*Presbytis melanophos*, *Semnopithecus cristatus*), 6 wild boar (*Sus* sp.), 6 pangolins (*Manis javanica*), a moonrat (*Echinosorex gymnurus*), 2 monitor lizards (*Varanus salvator*) and 8 domestic chickens (Shine et al., 1998a). At this site, small snakes fed largely on rats and shifted to larger prey at 3–4 m body length. In more disturbed areas in North Sumatra, even larger individuals ate some rats, mostly commensals from agricultural and village habitats (Shine et al., 1999). Other prey reported for this species include: fully grown barking deer (*Muntiacus muntjak*, 14 kg) (Nettelbeck, 1995), domestic pigs and goats (Groombridge & Luxmoore, 1991), an adult Sulawesi pig (*Sus celebensis*, <70 kg) (Auliya, 2003), a 23-kg adult female sun bear (Fredriksson, 2005), domestic dogs, cats and two black swans from a lake (Ridley, 1899), a slow loris (*Nycticebus coucang*) (Wiens & Zitzmann, 1999), pangolins, and a human teenager (Murphy & Henderson, 1997). There are less reliable reports of leopards and a fully-grown sambar deer (Murphy & Henderson, 1997). Adult humans have been killed, but apparently not fully ingested.

The second largest species, *Python molurus*, coexists with *B. reticulatus* in parts of Southeast Asia and also occupies most of the remainder of the Region. Although shorter than *B. reticulatus*, it is heavily built and large individuals can attain >70 kg and take similar-sized prey (e.g. Groombridge & Luxmoore, 1991; Murphy & Henderson, 1997; Zhao et al., 1998; Daniel, 2002). Reported stomach contents include: frogs, monitor lizards, birds, bats, rodents, pangolins, porcupines, langurs, jackals, mousedeer, hog deer (*Axis porcinus*, 45 kg), chital, barking deer, pigs, chinkara, civets and leopards. Infrared-detecting pit organs on the lips of *P. molurus* are most sensitive in the 8–12 μm range, which matches the infrared emissions from mammals and birds (Grace et al., 1999). As in the pitvipers, detection is by a thermal rather than photochemical mechanism (Gracheva et al., 2010). Infrared and visual information is overlain on the optic tectum and these snakes can target prey accurately with their eyes covered. When a prey is captured there is a huge (> 5×) increase in the metabolic rate of the snake and large increases in the mass of most internal organs, which atrophy in the weeks or even months between meals (Secor, 2008). The smaller pythons, *P. breitensteini* (<2 m, 20 kg), *P. brongersmai* (<2.6 m, 22 kg) and *P. curtus* (<2m, 18 kg), are confined to equatorial Southeast Asia and apparently feed mostly on rats (Stuebing & Inger, 1999; Keogh et al., 2001). Large individuals of the brown morph of *P. brongersmai* in Northeast Sumatra ate more non-rodent mammalian prey (slow loris, civets, tree shrew, and yellow-throated marten) than the other three morphs (Shine et al., 1998b).

Pythons in the Australasian genera *Liasis* and *Morelia* (scrub pythons) penetrate the extreme east of the Region, where *Morelia* co-occurs with *B. reticulatus* on some Moluccan islands (Harvey et al., 2000). *M. clastolepis* on Ambon and Seram can reach 4 m and one had a cuscus (Phalangeridae) in its stomach. *M. tracyae* on Halmahera attains at least 2.5 m and was reported by local collectors to feed on fruit bats.

***Boidae*. –** Boids, like pythons, kill by constriction. The Papuan-Pacific genus *Candoia* is represented on the eastern fringes of the Region by members of the *C. carinata* complex. These are semi-arboreal snakes, with a maximum length of around a metre. A sample of 98 prey items from 207 museum specimens (of unspecified geographic provenance) included 78 skinks, 3 frogs, 4 mice, 4 rats and 2 New Guinea bandicoots (Harlow & Shine, 1992). Larger specimens were more likely to contain mammalian prey. The Afro-Indian genus *Eryx* is represented in the western half of the Region by four species. They are mostly medium-sized (<1 m), nocturnal, burrowing snakes of semi-desert and steppe, although *E. conicus* also occurs in forest in India. Reported dietary items include frogs, lizards, shrews, rodents and various ground birds, including hoopoes (Minton, 1966; Sharma & Vazirani, 1977; Rodriguez-Robles et al., 1999; Daniel, 2002; Schleich & Kästle, 2002; Khan, 2002).

***Colubroidea*. –** All the remaining snakes are in the superfamily Colubroidea (or Caenophidia), which includes 188 of the 240 snake species recorded from Sundaland (Malay Peninsula, Borneo, Sumatra, Java and Sulawesi) (Inger & Voris, 2001). The use of venom by colubroids to subdue prey, rather than constriction, may have allowed muscle specialisation for more rapid locomotion, although many venomous species are slow-moving ambush foragers and some venomous colubroids use constriction (Greene, 1989b). I have largely followed the classification into families and subfamilies suggested by Lawson et al. (2005), who recognises five major groups within the colubroids. Venom delivery systems vary greatly within and between subfamilies, but the venom-secreting glands and some of the venoms apparently originated in the common ancestor of snakes and anguimorph and iguanian lizards (Fry et al., 2006). The characterisation of the majority of colubroids that lack front fangs as "rear-fanged" hides a great variety of venom delivery systems (Pough et al., 2004; Deufel & Cundall, 2006). Recent work has also begun to

reveal the diversity in the composition of colubroids venoms, with evidence for pronounced taxon-specific toxicity and correlated ontogenetic and geographical shifts in diet and venom composition (Mackessy et al., 2006), but the role of the venom in prey capture by rear-fanged species is still very poorly understood.

Pareatidae. **–** *Aplopeltura boa* (<85 cm) is a nocturnal, arboreal snake which feeds on lizards and snails (David & Vogel, 1996; Stuebing & Inger, 1999).

Viperidae-Crotalinae. **–** Viperids are stout-bodied, wide-gaped, snakes that inject venom through long, anterior fangs, which fold backwards when not in use (Pough et al., 2004). Viperid venom not only immobilises the prey but also contains powerful digestive enzymes that start the process of tissue breakdown. Pitvipers are found throughout the Region, except the most arid areas. They have paired infrared-sensitive pits between the nostril and the eyes. This infrared detection system, which evolved independently of the less senstive system in the pythons, allows pitvipers to accurately target endothermic prey in the dark (Safer & Grace, 2004). All pitvipers are venomous and many feed on relatively large prey, although only a few species exceed 130 cm in length. The largest species, *Zhaoermia mangshanesis,* from Hunan, China, can reach more than 2.1 m in length and 5 kg in weight (Mebs et al., 2006). All appear to be mainly ambush predators, but many also take prey, such as bird nestlings, which suggest active foraging. Some species are strictly terrestrial or arboreal, while others use both habitats. Terrestrial crotalines feeding on mammals may inject venom and then release the dying prey, which is followed by the scent trail (Waters et al., 1996), but snakes feeding on birds or in trees do not release their prey. Although some crotalines elsewhere are known to be dietary specialists, many Oriental species for which information is available appear to take a wide range of prey. However, in many species, the major prey varies with age/size and season (Orlov et al*.,* 2002), so simply listing all recorded prey items for a species may give a misleading impression. Most species are reported to take small mammals as adults, but birds, frogs and lizards are also mentioned for most, and sometimes also fish and snakes (Pope, 1935; Mao, 1970; David & Vogel, 1996; Lee & Lue, 1996; Zhao et al., 1998; Stuebing & Inger, 1999; Daniel, 2002; Schleich & Kästle, 2002; Orlov et al., 2002). Frogs are the most frequently reported prey for juveniles and are the commonest prey for adults of some species (e.g. Creer et al., 2002). Two Oriental species have been relatively well studied.

The Malayan pitviper, *Calloselasma rhodostoma*, is a terrestrial species, <1m in length, which is common in lowland forests, plantations and gardens in much of Southeast Asia. A total of 225 prey items recovered from faeces, regurgitates and stomach contents, included invertebrates (centipedes and beetles), fish, frogs, lizards, skinks, geckoes, colubrid snakes, birds and rodents (Daltry, Wüster & Thorpe, 1998a). In most regions, the snakes shift from ectothermic prey (mostly amphibians and reptiles) to mammals and birds at body lengths greater than 40 cm, but the reverse happens in North and West Thailand. The young snakes use caudal luring with their modified tail tips, which presumably attracts insectivores. Venom composition varies considerably over the range of the species and this geographical variation correlates with the variation in diet (Daltry et al., 1996). Studies on captive-bred snakes show that venom composition is under genetic control, suggesting that the variation represents local adaptation to dealing with prey animals that differ in their susceptibility to the various venom components. *C. rhodostoma* typically lies coiled and motionless on the ground and is, as a result, the leading cause of venomous snakebites to people in many areas (Daltry et al., 1998b).

The habu, *Protobothrops flavoviridis,* inhabits the Ryukyu Islands, at the northern margins of the Region and reaches a maximum length of 2.3 m (Mishima et al., 1999). A sample of 927 prey items from habu stomachs on the Amami Islands included 43 species in 27 families, but was dominated by rodents, of which 82.5% were the abundant commensal rat, *Rattus tanezumi*. Birds, reptiles (including other habu), amphibians and fishes were also eaten, and birds dominated the diet on an island lacking rodents (Katsuren et al., 1979 in Mishima et al., 1999). Most prey is caught from ambushes although the success of live-baited traps suggests that they also actively search for prey. Young habus eat more lizards, amphibians and shrews. Captive habu can survive >3 years without eating. The habu is nocturnal and partly arboreal, and is inactive for most of the winter. It thrives in human-dominated landscapes, where rats are abundant, and is responsible for numerous bites of humans. The smaller (<50 cm) himehabu, *Ovophis okinavensis*, has a similar diet to the habu (Mori & Moriguchi, 1988). In the northern hills of Okinawa Island (27°N), this species is active at night in winter, allowing it to feed heavily on two species of frogs that aggregate to breed at this time (Mori et al., 2002).

Viperidae-Azemiopinae. **–** *Azemiops feae* is reported to feed on small mammals (Orlov et al., 2002).

Viperidae-Viperinae. **–** The true (pit-less) vipers are a largely African and Palaearctic subfamily, but there are five Oriental species, three of which reach their eastern limits in Pakistan. Russel's viper, *Daboia* (*Vipera*) *russelii* is widespread in the Region, from Pakistan to Sri Lanka, China and parts of Indonesia, and is found in a variety of habitats. It is the most common cause of fatal snakebites in India and is reported to feed mainly on rats, although it also eats birds, frogs, lizards and other snakes (Pope, 1935; Lee & Lue, 1996; Zhao et al., 1998; Daniel, 2002). The saw-tailed viper, *Echis carinatus*, is widespread in dry habitats in the western half of the Region. Stomach contents have included invertebrates, frogs, toads, geckos, and a striped palm squirrel (*Funambulus*) (Minton, 1966; Sharma & Vazirani, 1977).

Elapidae-Elapinae. **–** The elapines (the traditional family Elapidae) are a pantropical subfamily of venomous snakes. Although front-fanged like the vipers, most elapines have shorter, immobile fangs that remain erect when the mouth is shut (Pough et al., 2004). Their venoms generally have fewer components and are primarily neurotoxic. Compared

with vipers, elapines also have relatively narrow gapes and, usually, bodies, and take mostly elongate prey, although defensive bites cause many human deaths in the Region. Unlike vipers, most are active foragers, usually on the ground. In the Region, this subfamily is represented by the coral snakes, kraits and cobras. The coral snakes (*Calliophis*, *Sinomicrurus* and *Hemibungarus*) are slender, nocturnal, semi-fossorial snakes found mostly in forests. They feed largely on small snakes and lizards (Mori & Moriguchi, 1988; David & Vogel, 1996; Zhao et al., 1998; Stuebing & Inger, 1999). The kraits (*Bungarus*) are bigger snakes (some species <2 m in length) which feed mainly on snakes, as well as lizards and amphibians, and also, in at least some species, small mammals (Pope, 1935; Minton, 1966; David & Vogel, 1996; Lee & Lue, 1998; Zhao et al., 1998; Stuebing & Inger, 1999; Daniel, 2002; Schleich & Kästle, 2002; Khan, 2002). In Taiwan, smaller individuals of *B. multicinctus* ate mainly fish and large ones preferred snakes (Mao, 1970). The cobras (*Naja*) are medium-sized (<1.6 m) snakes found in all habitats from forest to urban areas. They are reported to consume mostly rodents, but also eat birds and their eggs, lizards, frogs, fish and other snakes (Pope, 1935; Minton, 1966; Mao, 1970; David & Vogel, 1996; Zhao et al., 1998; Stuebing & Inger, 1999; Daniel, 2002). Prey remains in 84 *N. sputatrix* guts examined in Java were mostly (59%) mammalian, presumably rats, and the remainder probably frogs (Boeadi et al., 1998). Cobra bites have caused many human fatalities. The king cobra, *Ophiophagus hannah*, is a swift-moving diurnal snake that can attain a maximum of 6 m in length, making it the largest venomous snake in the world. It feeds mostly on other snakes (especially large individuals of *Python* and *Ptyas*; David & Vogel, 1996) but will also take large lizards (Stuebing & Inger, 1999) and, occasionally, birds and rodents (Zhao et al., 1998).

Elapidae-Psammophiinae. – The Asian sandsnake, *Psammophis condanarus*, is a small (<1 m), diurnal snake of open habitats that feeds on lizards, frogs and occasionally other snakes (Daniel, 2002; Schleich & Kästle, 2002). In Pakistan, this species and *P. leithii* climb into bushes and small trees to feed on nestlings and eggs (Khan, 2002). *P. schokari* is reported to reach a speed of 16 km hr^{-1} (Firouz, 2005).

Elapidae-Xenodermatinae. – *Xenodermus javanicus* is a small, nocturnal, terrestrial snake, which is usually found near water and feeds on frogs (David & Vogel, 1996; Stuebing & Inger, 1999).

Elapidae insertae sedis. – The Asian mock viper, *Psammodynastes pulverulentus*, is a small, rear-fanged snake that kills using constriction and venom (Greene, 1989b). A total of 113 prey items from specimens across its geographical range included 58% skinks, 13% other lizards, 23% frogs and 6% colubrid snakes. The enlarged anterior teeth appear to help trap slippery, muscular skinks in the mouth.

Colubridae-Calamariinae. – The reedsnakes are a diverse group of poorly-known, small, semi-fossorial snakes, which are believed to feed mainly on invertebrates, but one of the largest species, *Calamaria lumbricoidea* (<42 cm), is also reported to take skinks (David & Vogel, 1996).

Colubridae-Colubrinae. – For most of the 101 genera included in this group by Lawson et al. (2005), there is either no published dietary information or they are reported to feed on a variety of small vertebrates. Most colubrine prey seem to be small relative to snake body mass (mean relative prey masses 0.11–0.33 for 10, mostly American, species; Rodríguez-Robles, 2002). Lizards and frogs are the most frequently reported prey in the Region, but the diets of most relatively well-studied species also include endotherms. Most appear to be active foragers, although some also use ambush techniques. Venom-delivery systems vary hugely and some are considered non-venomous. In the absence of a detailed phylogeny, only the better-studied and/or most distinctive genera are treated separately here, in alphabetical order except where related genera are grouped.

The vinesnakes, *Ahaetulla*, are medium-sized (<2 m), diurnal, slender, long-snouted, arboreal snakes. The enlarged front teeth on the lower jaws help to grip skinks (Greene, 1997), although *A. prasina* is also reported to eat other lizards and frogs (Zhao et al., 1998; Stuebing & Inger, 1999) and *A. nasuta* takes small mammals and birds (Daniel, 2002).

The >20 species of cat snakes, *Boiga*, range from tropical Africa to Australia. They are medium to large (<3 m and 2 kg in the biggest species), slender, large-headed snakes with large eyes and vertical elliptical pupils. They are nocturnal and the Oriental species are all at least partly arboreal. The brown tree snake, *Boiga irregularis*, has been intensively studied on the Pacific island of Guam, where it was introduced around 1950 and has subsequently extirpated most of the indigenous forest vertebrates (Rodda et al., 1999). Snakes assigned to this species are also found in Sulawesi and the Moluccas in the Region. In Guam, *B. irregularis* uses both slow, systematic searching and ambush techniques to prey on all available vertebrates, occasionally up to 70% of its own mass (Rodda et al., 1999). Larger snakes eat more endotherms. They climb well but the largest individuals (<3.1 m) are usually found on the ground. Both visual and olfactory cues are used to locate prey, which is then swallowed directly if small or killed by constriction if large. The role of the venom that is delivered with their rear fangs is unclear, since surgically deprived snakes can still kill prey, but in the laboratory lizards and birds are 10–30 times more susceptible than mice (Mackessy et al., 2006). It also actively forages for carrion (Shivik & Clark, 1999).

The available information on other Oriental *Boiga* species, including stomach contents for 18 species (Greene, 1989a), is consistent with their having broadly similar ecologies to *B. irregularis*. Most species appear to have broad diets, with smaller species and smaller individuals of larger species preying mostly on diurnal arboreal lizards and larger ones taking more mammals and/or birds (Minton, 1966; Sharma & Vazirani, 1977; David & Vogel, 1996; Lee & Lue, 1996; Zhao et al., 1998; Stuebing & Inger, 1999; Daniel, 2002). Most prey consists of inactive animals found through active

searching. *Boiga cynodon*, has 'extraordinarily long' teeth, which may be an adaptation for penetrating the feathers of birds (Stuebing & Inger, 1999), which made up 12 of 20 items in 19 stomachs (Greene, 1989a). Prey reported for *B. dendrophila* ranges from fish, frogs, snakes and lizards to birds, rodents, cave-roosting bats and an adult mouse deer (*Tragulus javanicus*, 3 kg), swallowed head first by a 1.7 m specimen (Greene, 1989a, 1997). *Boiga cyanea* in Nepal includes venomous snakes in its diet (Schleich & Kästle 2002).

Uniquely among snakes, the flying or tree snakes, *Chrysopelea*, move between trees in a controlled glide, with their descent slowed by a concavity formed with the aid of longitudinal hinges on the ventral scales (Greene, 1997). These big-eyed diurnal snakes feed largely on lizards (Lim, 1967; Pope, 1935; Stuebing & Inger, 1999), but also take frogs, snakes, small birds, bats and small mammals (David & Vogel, 1996; Zhao et al., 1998; Daniel, 2002; Schleich & Kästle, 2002).

Several species of Old World racers, previously placed in the Holarctic genus *Coluber*, enter the Region in Pakistan and India, where they consume a variety of small vertebrates, including lizards, young birds and small mammals (Minton, 1966; Sharma & Vazirani, 1977; Daniel, 2002; Khan, 2002). *Spalerosophis diadema* has been observed going from burrow to burrow in fields to look for rodents, as well as chasing squirrels (*Funambulus*) in a tree (Sharma & Vazirani, 1977).

The Indian egg-eating snake, *Elachistodon westermanni*, is a small snake (<80 cm) of northern India and Nepal, in which an enlargement of the throat vertebrae breaks the shell of an egg after it has been swallowed (Daniel, 2002). However, the grooved teeth and deep nasal pits, which are thought to be infrared sensitive, suggest it also takes endothermic prey (Schleich & Kästle, 2002).

The racers or ratsnakes, *Elaphe*, and the related genera *Coelognathus*, *Gonyophis* and *Gonysoma*, are medium to large (<2.7 m), active, terrestrial and arboreal, diurnal or crepuscular, non-venomous snakes that kill by constriction. The adults of most species prey largely on small mammals, including rats, squirrels and, especially on *E. taeniura*, cave-roosting bats, and several also take birds (Pope, 1935; David & Vogel, 1996; Zhao et al., 1998; Stuebing & Inger, 1999; Daniel, 2002; Helfenberger, 2002 [in Schleich & Kästle, 2002]). Juveniles feed on lizards and amphibians. *E. carinata* apparently feeds largely on snakes, but also takes frogs, lizards, birds, rats and eggs (Zhao et al., 1998). The relatively small (SVL <1 m) *E. quadrivirgata* on Yakushima Island (30°N) fed entirely on reptiles, mostly skinks (Tanaka & Ota, 2002). The ratsnakes, *Ptyas* (including *Zaocys*), are slender, medium to large, fast-moving diurnal snakes. *Ptyas carinatus* (<4 m) is the longest snake in Asia after the pythons and king cobra. It is mainly terrestrial but can also climb and swim, and feeds on large frogs and small mammals, especially rats (David & Vogel, 1996). Out of 85 guts of *Ptyas mucosus* examined in Java, 65 had prey remains, most probably of frogs but nine contained mammal fur, probably from rats (Boeadi et al., 1998). In other parts of the Region, this species has been reported to also eat lizards, birds, bats and other snakes (Pope, 1935; Minton, 1966; David & Vogel, 1996; Zhao et al., 1998; Daniel, 2002). In Rajasthan, India, one was observed chasing a rat "at speed", which was then killed by constriction (Sharma & Vazirani, 1977). In Pakistan, Khan (2002) reported one individual eating 18–22 full-sized *Euphlyctis* frogs. Other species of *Ptyas* apparently have similar diets (Zhao et al., 1998; Schleich & Kästle, 2002).

The wolfsnakes, *Lycodon*, are nocturnal, terrestrial and/or arboreal snakes with enlarged front teeth and other cranial modifications for eating skinks (Greene, 1997; Jackson & Fritts, 2004). Skinks or other lizards are mentioned for all species with dietary information, with frogs, snakes, birds, mice or rats also taken by some species (Pope, 1935; Minton, 1966; David & Vogel, 1996; Zhao et al., 1998; Stuebing & Inger, 1999; Daniel, 2002; Schleich & Kästle, 2002; Jackson & Fritts, 2004). Introduced *Lycodon aulicus* have had a devastating impact on populations of native skinks in the Mascarene Islands (Jackson & Fritts, 2004).

The many Oriental species of kukri snakes, *Oligodon*, are small (<1 m) snakes with enlarged rear fangs, used to slice into leathery reptile eggs (Pough et al., 2004). In addition to eggs, they are reported to feed on frogs, lizards (including skinks), snakes, small mammals and birds (Minton, 1966; Lim, 1967; Ota & Lin, 1994; David & Vogel, 1996; Greene, 1997; Zhao et al., 1998; Stuebing & Inger, 1999; Schleich & Kästle, 2002). On Orchid Island, off Taiwan, females of *O. formosanus* vigorously defend turtle nests against conspecifics over several weeks (Huang et al., 2011).

The litter snakes, *Sibynophis*, are small (<1 m) snakes of the forest floor that are reported to feed on skinks and other lizards, frogs and insects (David & Vogel, 1996; Stuebing & Inger, 1999; Schleich & Kästle, 2002). They have hinged teeth, like young *Xenopeltis*, apparently as a convergent adaptation to feeding on skinks (Pough et al., 2004).

The brown snakes, *Xenelaphis*, are large (<2.5 m), actively foraging, terrestrial snakes. *Xenelaphis hexagonotus* is reported to feed largely on rats, but also consumes frogs, birds and sometimes fish (David & Vogel, 1996; Stuebing & Inger, 1999).

***Colubridae-Natricinae.* –** Oriental natricines are relatively small snakes (mostly <1 m) that range from fully aquatic to largely terrestrial. Frogs are a major component of the diet of most species (in the genera *Amphiesma*, *Atretium*, *Macropisthodon, Rhabdophis*, *Sinonatrix* and *Xenochrophis*) for which adequate information is available (Pope, 1935; Minton, 1966; Lim, 1967; Devi, 1991; David & Vogel, 1996; Lee & Lue, 1996; Ota & Iwanaga, 1997; Mori & Moriguchi, 1998; Zhao et al., 1998; Stuebing & Inger, 1999; Daniel, 2002; Tanaka & Ota, 2002). Tadpoles and fish are also eaten by the more aquatic species and lizards are mentioned for several species. *Rhabdophis chrysargos* is reported to also take small mammals (David & Vogel,

1996) and *Amphiesma stolatum* in Pakistan to take rodents and birds (Khan, 2002).

***Colubridae-Pseudoxenodontinae*. –** Species of *Pseudoxenodon* are medium-sized forest snakes that appear to feed largely on frogs (David & Vogel, 1996; Zhao et al., 1998; Schleich & Kästle, 2002).

***Colubridae-Xenodontinae insertae sedis.* –** The Sri Lankan wolf snake, *Cercaspis carinatus*, is a nocturnal, terrestrial snake of damp forests that is reported to feed on geckoes, skinks and other snakes (De Silva, 1990). Little is known about the biology of most other genera tentatively included in this group by Lawson et al. (2005).

Crocodilians

Crocodiles include the largest living reptiles, with the biggest Oriental species, *Crocodylus porosus* and *Gavialis gangeticus*, occasionally exceeding 6 m in length and, at least in the former species, 1000 kg in body mass (Britton, 2003). All living species are more or less aquatic and forage mostly in water or by ambushing prey at the water's edge. Drowning is often used to kill large prey. Prey is not chewed: small prey is swallowed whole while large prey must be dismembered first. Most species will also take carrion.

***Crocodylidae*. –** The Region supports four species of *Crocodylus*. *Crocodylus mindorensis*, in the Philippines, and *C. siamensis,* from Borneo to Myanmar and Vietnam, are highly endangered, relatively small (usually <3 m), freshwater species. Little is known about the ecology of either species. *Crocodylus siamensis* is reported to feed largely on fish, but also amphibians, reptiles and possibly small mammals (Ross, 1998). The mugger, *C. palustris*, is a larger species (<5 m) with the broadest snout of any Oriental crocodilian. It was once widespread in a variety of freshwater habitats from Iran to Bangladesh and south to Sri Lanka, but is now increasingly restricted. Subadults feed largely on fish, amphibians and arthropods, but adults have a broad diet that includes fish, amphibians, turtles, snakes, waterbirds and a wide variety of mammals, including monkeys, deer and wild boar, as well as domestic dogs, pigs, cattle, sheep and goats (Kumar et al., 1995; Santiapillai et al., 2000; Daniel, 2002; Schleich & Kästle, 2002; Bhatnagar & Mahur, 2010). Humans are occasionally eaten. Carrion is regularly taken and is pulled into the water where possible. The saltwater crocodile, *C. porosus*, is the largest living reptile (< 7m) and occurs throughout most of the Region in both brackish and fresh water, although usually near the sea. The diversity of the diet increases with age and includes a variety of vertebrates, from fish and turtles to snakes, birds and mammals. Large adults occasionally take larger mammalian prey, including domestic livestock, wild boar, monkeys and people, and, in Australia, feral water buffalo, cattle and horses (Kar & Bustard, 1983; Webb & Manolis, 1989; Daniel, 2002). Even juveniles can take surprisingly large prey, with individuals 136-179 cm in length and weighing 8.7–15.8 kg taking domestic goats 50-92% of their own weight in Orissa, India (Kar & Bustard, 1983).

***Gavialidae*. –** The true (*Gavialis gangeticus*) and false (*Tomistoma schlegelii*) gharials have similar long narrow snouts. *Gavialis* inhabits quiet pools in deep, fast-flowing rivers from Pakistan to Myanmar. It is the most fully aquatic of crocodilians and leaves the water only to bask and nest. Adults feed mostly on fish, but large individuals have also been known to take turtles, waterfowl, small mammals, and, reportedly, dogs and goats (Daniel, 2002; Schleich & Kästle, 2002). *Tomistoma* inhabits freshwater swamp forests, lakes and quiet rivers in Southeast Asia. Although not reported to grow as large as *Gavialis*, it appears to have a broader diet including, in addition to fish, insects and crustaceans, mammals as large as an immature macaque and an adult male proboscis monkey (*Nasalis larvatus*) weighing c. 20 kg taken from a low branch by a 3.5-m *Tomistoma* (Galdikas & Yeager, 1984).

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Any bird that eats terrestrial invertebrates will presumably also consume juvenile vertebrates in the same size range. The consumption of larger vertebrates has also been widely reported for Oriental birds and has, no doubt, been overlooked in others. However, bird species for which terrestrial vertebrates form a significant proportion of the diet are confined to a few families. Vertebrate consumption by birds from other families is dealt with under "other non-passerines" and "other passerines".

Non-passerines

***Picidae*. –** Despite their specialisations for excavating wood, most woodpeckers are more or less omnivorous and the consumption of nestlings, lizards and frogs has been recorded in several Oriental species (Winkler et al., 1995).

***Megalaimidae*. –** Asian barbets are highly frugivorous (Corlett, 1998), but some small vertebrates, such as lizards and tree frogs, are also taken, especially when feeding nestlings (Short & Horne, 2001).

***Bucerotidae.* –** The hornbill's long bill extends into the visual field, allowing a precision-grasping technique that is very different from the pecking or lunge-and-grab technique of most birds (Martin & Coetzee, 2004). This not only enables these heavy birds to pluck fruits that would otherwise be beyond their reach, but also makes many hornbill species efficient predators (Kemp & Woodcock, 1995). The degree of carnivory reported varies greatly between the Oriental species, but some species spend much of their time hunting for animal prey. The most commonly reported vertebrate prey are lizards and the contents of tree holes, including bird eggs, nestlings, bats and flying squirrels, but some species also hunt diurnal squirrels and adult birds, as well as frogs, snakes, rats and mice (Kemp & Woodcock, 1995; Kannan & James, 1997; Mudappa, 2000; Harikumar et al., 2001).

***Coraciidae*. –** The *Coracias* rollers are sit-and-wait predators of open habitats, feeding on large invertebrates and small vertebrates, including frogs, lizards, snakes, mice, shrews and young birds (Roberts, 1991; Fry et al., 1992).

***Alcedinidae*. –** The Oriental kingfishers are mostly sit-and-wait predators that hunt from a perch in forest. Diets of different species range from fully aquatic to fully terrestrial. The terrestrial component typically consists of large invertebrates plus a variable number of small vertebrates, including frogs, lizards and, in the larger species, snakes, rodents and nestlings (Fry et al., 1992; Smythies & Davison, 1999).

***Cuculidae*. –** Most cuckoos are basically insectivorous, but many species also appear to be opportunistic predators on small vertebrates (Roberts, 1991; Payne, 2005). Frogs, lizards and nestlings are most commonly mentioned, but there are also reports of cuckoos taking snakes, small mammals and birds. Coucals (*Centropus*), in particular, are often mobbed by small birds, suggesting that they are significant nest predators, but frogs, lizards and snakes were more important in the diet of *C. sinensis* in a South Indian village (Natarajan, 1992). *Centropus sinensis* in Hong Kong ate a 60-cm pitviper (Carey et al., 2001). A chestnut-bellied malkoha in Singapore fed a flying lizard (*Draco*) to its chick (Lok & Lee, 2008).

***Tytonidae*. –** The owls are a monophyletic group, but molecular data suggests a deep divergence between the two families, Tytonidae and Strigidae, in the order Strigiformes (Wink et al., 2009). Large, forward-directed, rod-dominated eyes, highly developed acoustical senses, noiseless flight and powerful talons make owls the nocturnal counterpart of the diurnal birds of prey (Falconiformes). The Oriental barn owls (Tytonidae) are mostly poorly known forest birds, but the near-cosmopolitan *Tyto alba* (250–500 g) has been widely studied in the Region because of its importance in controlling populations of agricultural pest rodents. In captivity, it can capture prey in complete darkness using only acoustic cues (Schwab, 2003). Audio and visual information are combined in the brain into a single integrated spatial map. *Tyto alba* is mostly found in relatively open habitats, where it can hunt from a perch or from low flight, but it occurs in forest on some islands and has recently adapted to dense oil palm plantations in Malaysia (Lenton, 1984). Dietary studies in plantations and rice fields in Malaysia show an almost total reliance on *Rattus* spp. (<200 g) (Lenton, 1984; Lee, 1997; Hafidzi & Mohd Na'im, 2003), but in cultivated areas elsewhere in the Region other rodents (e.g. Mushtaq-Ul-Hassan et al., 2007) or shrews (Mahmood-ul-Hassan et al., 2007) dominate. Amphibians, passerine birds and microchiropteran bats are also significant at some sites. In contrast to the long, broad wings of *Tyto alba*, the oriental bay owl (*Phodilus badius*) has short, round wings that allow it to fly through thick vegetation (Duncan, 2003). It is reported to feed on a wide range of small vertebrates.

***Strigidae*. –** The true owls (Strigidae) are very diverse within the Region, in terms of both the number of species (63 spp., compared with seven Tytonidae: Inskipp et al., 1996) and the size range (50–2500 g: König et al., 1999). Females are usually larger and heavier than males. Some species are also active in daylight and a few are largely diurnal. All the Oriental species for which diets are known appear to be take a wide variety of prey, including species more than half their own weight.

The most speciose group is the scops owls (*Otus*), with around 23 Oriental species of small to medium-sized owls (c. 65–250 g). Most species are forest birds, although several also use more or less open habitats. Most species for which dietary information is available feed mainly on insects, but all also appear to consume some small vertebrates, including small rodents, birds, lizards and, in some species, bats (Marks et al., 1999; König et al., 1999; Carey et al., 2001; Verzhutskii & Ramanujam, 2002; Duncan, 2003). The *Glaucidium* owlets are also small (50–170 g) birds, in some cases at least partly diurnal, which can capture surprisingly large prey. Small birds, mice, lizards and insects are recorded for all species. *G. cuculoides* (150–175 g) has been seen to catch common quail (100 g) in flight and the tiny *G. brodiei* (60 g) can capture adult barbets, woodpeckers and thrushes (Marks et al., 1999; König et al., 1999; Duncan, 2003). The widespread spotted owlet (*Athene brama*) (110 g) hunts from a perch in open habitats in which it captures large insects and small mammals (particularly *Mus* spp. at several sites), as well as sparrow-sized birds, microchiropteran bats, lizards and frogs (Shah & Beg, 2001; Mushtaq-Ul-Hassan et al., 2003; Ramanujam & Verzhutskii, 2004a). The larger (240 g) and highly endangered forest owlet (*A. blewitti*) is reported to feed on skinks, other lizards and small rodents (Ishtiaq et al., 2002; Ishtiaq & Rahmani, 2005).

At the other end of the size range are the eagle-owls (*Bubo*), with the largest species, *B. bubo*, in the north of the Region, attaining 2–3 kg. Among the larger prey items recorded for this species are deer fawns, lambs, large flying squirrels and adult hares, as well as birds, including owls, buzzards and herons (Marks et al., 1999; König et al., 1999; Zahler & Dietemann, 1999; Duncan, 2003). The somewhat smaller forest species, *B. nipalensis*, takes mostly large birds, including jungle fowl, pea-fowl and pheasants, but also mammals, including hares, jackals, deer fawns (*Muntiacus muntjac*), giant squirrels (*Ratufa indica*: Kannan, 1994) and reptiles. *Bubo coromandus*, an owl of open habitats, will hunt in daylight, especially on cloudy days, and takes birds, especially crows (*Corvus* spp.), as well as rats, hares, squirrels, reptiles and amphibians. The diet of *B. bengalensis* in disturbed habitats in southern India was dominated by nocturnal rodents (mostly <200 g) at most sites, but the author suggests that these may be partly a substitute for hares (*Lepus nigricollis*, 4 kg), which were the preferred prey at a site where they had not been depleted by hunting (Ramanujam, 2005), and are also consumed by other Oriental eagle-owls. Other prey for this species included birds (including a *Milvus migrans*), reptiles, frogs and arthropods. The closely related fish-owls (*Ketupa*) consume fish and frogs as well as a similar range of other vertebrates.

The Oriental wood-owls (*Strix*: 500–1200 g) feed on rodents, birds and lizards (Marks et al., 1999; König et al., 1999; Duncan, 2003; Samarwickrama et al., 2006). The diets of the Oriental species of hawk-owl (*Ninox*) are reported to include flying insects and a wide variety of small vertebrates, including bats. The long-eared and short-eared owls (*Asio*) are winter visitors to the Region and are reported to feed mostly on mammals (e.g. Mushtaq-Ul-Hassan et al., 2007).

***Pandionidae*. –** The almost cosmopolitan osprey, *Pandion haliaetus*, feeds almost entirely on live fish, although there are occasional reports of it taking a wide range of other small vertebrates (Roberts, 1991; Ferguson-Lees & Christie, 2001).

***Accipitridae*. –** The Accipitridae is a large and diverse family, with more than 80 species in the Region. Recent molecular studies have gone a long way towards resolving the internal phylogeny of the family (Lerner & Mindell, 2005; Griffiths et al., 2007), which was previously confused by morphological convergence, although the positions of some genera are still uncertain.

The rather falcon-like *Elanus* kites (Elaninae) are a basal group. The black-shouldered kite, *E. caeruleus* (200–350 g) is widespread in open habitats in the Region, including areas recently cleared of forest. It specialises on small mammals (<90 g), particularly diurnal rodents, but is also reported to take small birds, lizards, snakes, frogs and insects (Roberts, 1991; Ferguson-Lees & Christie, 2001).

The bazas (*Aviceda*) (Perninae) occupy forest, edge and more open habitats in the eastern half of the Region. They hunt from a perch, taking large insects, lizards, snakes, and a variety of other small vertebrates from the ground or vegetation (Ali & Ripley, 1978; Ferguson-Lees & Christie, 2001; Carey et al., 2001). The Oriental species of honey-buzzards (*Pernis*, 2–4 spp.) (500–1500 g) feed largely on the combs, larvae, pupae and adults of social wasps and bees, but they also eat other insects as well as frogs, reptiles, small mammals and small birds (Roberts, 1991; Ferguson-Lees & Christie, 2001). The bat hawk, *Macheiramphus alcinus*, is a medium-sized (600 g) kite with a weak bill but huge gape that enables it to swallow small bats (mostly 20–75 g) and birds (particularly cave-nesting swiftlets) very rapidly in flight (Ferguson-Lees & Christie, 2001). Occasionally larger bats or birds may be carried to a perch. Most prey is caught within 15–30 minutes at dusk, although they also hunt at dawn and by moonlight.

The black kite, *Milvus migrans* (Milvinae), is probably the commonest raptor on the planet. It is found in most types of habitat apart from dense forest and eats anything from carrion and human garbage to small mammals, birds, lizards, snakes, frogs and fish (Roberts, 1991; Ferguson-Lees & Christie, 2001). As with the following species, it is often not clear how much of the prey is sick or injured, but these birds are certainly capable of capturing healthy vertebrates. They usually forage in flight and take most food from the ground or water surface. The brahminy kite, *Haliastur indus*, occupies much of the Region, usually near the coast, rivers or wetlands. This species is mostly a scavenger, but also takes a variety of small vertebrates (Ali & Ripley 1978; Roberts, 1991; Ferguson-Lees & Christie, 2001; Sivakumar & Jayabalan, 2004).

Two of the Oriental vultures, the Egyptian vulture, *Neophron percnopterus*, and the lammergeier, *Gypaetus barbatus*, belong to a monophyletic group (Gypaetinae) separate from the other vultures. *Neophron* is a relatively small vulture that feeds largely by scavenging, but also takes occasional "smaller, young or injured vertebrates of all classes" (Ferguson-Lees & Christie, 2001). The lammergeier is a huge (<7 kg) vulture with a unique and specialised diet that includes large quantities of bones, dropped from a height onto rocks to break them open (Ferguson-Lees & Christie, 2001). The same treatment is used for tortoises, such as *Testudo horsfieldi* (Roberts, 1991). The lammergeier is also believed to take some live mammals and birds. None of the other Oriental vultures (*Gyps, Aegypius*; Aegypiinae) take live prey.

The short-toed snake-eagle, *Circaetus gallicus* (Circaetinae), occupies a variety of more or less open habitats in the western half of the Region. It feeds largely on snakes, including venomous species, but also some lizards and occasional frogs, mammals and birds (Roberts, 1991; Ferguson-Lees & Christie, 2001). It hunts mostly from flight. The serpent-eagles (*Spilornis*), in contrast, favour more or less wooded areas and hunt from a perch. The crested serpent-eagle, *S. cheela*, may be the most common and widespread raptor in the Region (Thiollay, 1998). It eats mainly snakes and lizards, but also the occasional small bird or mammal (Ferguson-Lees & Christie, 2001). The Andaman serpent-eagle, *S. elgini*, appears to have a more varied diet of snakes, birds, frogs, lizards and rats, while there is little information on the diets of the other Oriental species.

The Philippine or monkey-eating eagle, *Pithecophaga jefferyi*, is a relatively isolated species, apparently most closely related to the snake-eagles (Lerner & Mindell, 2005). It is a huge bird (<8 kg), with relatively short, broad wings and huge feet and claws: the most powerful of the Oriental raptors. In many ways it is the Oriental equivalent of the Neotropical harpy eagle and African crowned eagle, but in historical times it has been restricted to four Philippine islands, Luzon, Samar, Leyte and Mindanao. It is now critically endangered as a result of its apparent requirement for mature rainforest cover over more than half of the territory of each breeding pair (Bueser et al., 2003). Where it occurred it was the top predator, since the Philippines lacks large mammalian carnivores and *Broghammerus (Python) reticulatus* is probably introduced (Brown & Alcala, 1970). Reported prey ranged from a 10-g bat to a 14-kg deer, and included terrestrial species, but diets in most studies seem to be dominated by medium-sized vertebrates caught in the canopy, particularly colugos (*Cynocephalus volans*: 1–2 kg) and palm civets (*Paradoxurus hermaphroditus*: <4 kg), but also macaques (*Macaca fascicularis*: <7 kg), and a wide range of other vertebrates, including flying and tree squirrels,

rats, large birds (hornbills, owls, hawks), snakes and monitor lizards (Kennedy, 1977; Collar et al., 1999; Ferguson-Lees & Christie, 2001; Ibañez et al., 2003). It hunts mostly from a perch inside the canopy and pairs are said to hunt monkeys cooperatively.

The typical or booted eagles (Aquilinae) form a monophyletic group, but none of the major genera currently recognised are monophyletic (Lerner & Mindell, 2005). The hawk-eagles (*Spizaetus*) are medium to large forest eagles, but the larger species take most of their prey from the ground, hunting from a perch below the canopy (Ferguson-Lees & Christie, 2001). Reported terrestrial prey includes mammals up to the size of hares and the Javan stink badger (*Mydaus javanensis*), jungle fowl and pheasants, lizards and snakes (Ferguson-Lees & Christie, 2001; Nijman et al., 2002). Hawk-eagles also take arboreal prey and the Japanese subspecies of *S. nipalensis*, which is distinctly larger than Oriental members of the same species, can apparently kill adult macaques (*Macaca fuscata*, c.10 kg) (Iida, 1999). Only juvenile primates are reported as prey in the Region. Members of the genera *Aquila* and *Hieraaetus* are intermixed in the molecular phylogenies (Lerner & Mindell, 2005). The smaller Oriental eagles feed on large birds and small mammals (Ferguson-Lees & Christie, 2001). The larger species occupy more or less open habitats in the west and north of the Region. They are reported to consume a wide range of mammals, birds and reptiles, with the larger species generally taking larger prey (<2 kg) and the diet varying considerably between sites (Roberts, 1991; Ferguson-Lees & Christie, 2001). The Asian black eagle, *Ictinaetus malayensis*, is an aerial-foraging forest eagle that appears to specialise on the contents of birds' nests, often seized whole from tree tops, shrubs or the ground, but it also takes birds, small mammals and frogs (Ferguson-Lees & Christie, 2001).

The harriers (*Circus*; Circinae) are widespread winter visitors to the Region, except for *C. assimilis*, which is resident in Sulawesi. Harriers are birds of open habitats, which they typically quarter, flying low and slowly. Most reported prey are small (<100 g) diurnal mammals, terrestrial birds, lizards, frogs and insects, but there are scattered reports of larger prey (<1 kg) (Roberts, 1991; Clark, 1996; Ferguson-Lees & Christie, 2001; Verma, 2006; Luo et al. 2010).

The genus *Accipiter* (Accipitrinae; goshawks and sparrowhawks) is the largest in the family and in the Region, where 17 species are recorded. Most Oriental species are more or less sedentary forest birds, but several occur in more open habitats and four are winter visitors to the Region. The species differ mostly in size, with a >15-fold difference in weight (c. 80-1200 g) between the smallest Oriental males and the largest females (Ferguson-Lees & Christie, 2001). Birds and lizards are the most commonly reported vertebrate prey items in the Region, but rodents, bats, frogs and snakes are also widely eaten. Most species hunt from a concealed perch, but others have more varied hunting styles. In Taiwan, prey items brought to nests of the besra (*A. virgatus*) were dominated by small to medium-sized birds (particularly *Megalaima oorti* and *Pycnonotus sinensis*), but also included large insects, bats, a small rat, lizards, frogs and a 250-g bamboo partridge (Huang et al., 2004). At the other extreme, a large (c. 1 kg) northern goshawk (*A. gentilis*) flew off with a 1-year-old golden monkey (*Rhinopithecus roxellana*) in the Qinling Mountains on the extreme northern margins of the Region (Zhang et al., 1999).

The fish-eagles (*Haliaeetus* and *Icthyophaga*; Haliaeetinae) are birds of the coast or inland freshwater. Fish dominates the reported diets of most fish-eagles, but the larger species also take some birds (mostly aquatic), small mammals and reptiles (Roberts, 1991; Ferguson-Lees & Christie, 2001). *Haliaeetus leucogaster* is reported to snatch *Pteropus* bats from tree roosts.

The *Buteo* buzzards (Buteoninae) are medium-large (0.7–2 kg) birds of prey that enter the Region only in winter and mostly in the north. They prefer more or less open habitats and their diets are usually dominated by small mammals, although they also take lizards, snakes and a variable number of birds when available (Roberts, 1991; Ferguson-Lees & Christie, 2001). The buzzard-hawks (*Butastur*) are represented by three species in the Region, two sedentary species with more or less complementary distributions in the east and west, and *B. indicus*, which winters in Southeast Asia. These are relatively small (300–400 g) raptors that usually hunt from a perch and take a variety of small vertebrates and large invertebrates from the ground (Ferguson-Lees & Christie, 2001). Reported vertebrate prey includes frogs, small snakes, lizards and small mammals up to the size of hares.

***Falconidae.* –** The falcons are the less diverse of the two families of diurnal raptors (c. 22 Oriental species vs. 82 Accipitridae). The *Microhierax* falconets are tiny (30–75 g) raptors of forest, forest edges and clearings (Kemp & Crowe, 1994). All species seem to feed predominately on large insects, hunted from a perch, but most are also recorded to take small birds, sometimes larger than themselves and usually in flight, as well as lizards and small mammals (Ferguson-Lees & Christie, 2001; Sivakumar et al., 2004). The white-rumped pygmy falcon, *Polihierax insignis*, is a somewhat larger (85–110 g), shrike-like falcon found in relatively open forest in mainland Southeast Asia. In contrast to the *Microhierax* falconets, it takes most prey from trunks, foliage or the ground (Kemp & Vidhidharm, 1998). In addition to large insects, lizards are important prey, particularly when breeding, and it also takes amphibians, small mammals and birds (Kemp & Vidhidharm, 1998; Ferguson-Lees & Christie, 2001).

The falcons (*Falco*) are larger raptors (170–900 g, with females larger than males), mostly found in more or less open habitats, although some hunt over forest. All species appear to be opportunistic hunters of small vertebrates, with a diet varying in space and time, but birds caught in flight dominate in several species, particularly the cosmopolitan peregrine falcon (*F. peregrinus*) (Roberts, 1991; Carey et al., 2001; Ferguson-Lees & Christie, 2001; Döttlinger, 2002). Large insects, lizards, rodents and bats are important in some species and areas.

Ardeidae. **–** Herons, egrets, bitterns and their relatives feed mainly on aquatic prey, but most Oriental species take small terrestrial vertebrates when the opportunity arises, although most records are from outside the Region (Mukherjee, 1971; Roberts, 1991; Martinez-Vilalta & Motis, 1992). Purple herons (*Ardea purpurea*) seem to have a predilection for snakes (Mukherjee, 1971; Prasad et al., 1993). The cattle egret (*Bubulcus ibis*) is the most terrestrial species, often feeding far from water.

Ciconiidae. **–** Most storks are largely aquatic, but most will also feed on land if food is available (Hancock et al., 1992). Frogs, reptiles, small mammals and the nestlings of ground-nesting birds are the most widely reported terrestrial vertebrate prey, but the black-necked stork (*Ephippiorhynchus asiaticus*) has been reported to catch and swallow whole adult coots, and one was seen to catch, kill and fly off with a pond heron (*Ardeola grayii*) in India (Breeden & Breeden, 1982; Hancock et al., 1992). Outside the Region, the white stork (*Ciconia ciconia*) has been seen to seize flying sparrows out of the air with its beak (Berthold, 2004).

Other non-passerines. **–** There are reports of at least occasional consumption of small terrestrial vertebrates for many Oriental non-passerines, although often from outside the Region, and other cases have certainly been overlooked, since diets are in general very poorly known. Most records refer to large ground-feeding birds, including pheasants (Phasianidae: Roberts, 1991; Madge & McGowan, 2002), bustards (Otididae: Roberts, 1991; Bhushan & Rahmani, 1992; Collar, 1996), cranes (Gruidae: Archibald & Meine, 1996), rails (Rallidae: Taylor & van Perlo, 1998) and ibises (Threskiornithidae: Roberts, 1991; Hancock et al., 1992). Rana (1988) reported that *Mus cervicolor* made up 16% of the gut contents of the Indian nightjar (*Caprimulgus asiaticus*, Caprimulgidae) in semi-desert Rajasthan.

Passerines

Laniidae. **–** Shrikes are relatively small (<100 g) passerines with raptor-like morphology, including a hooked bill, and strong legs and feet with sharp claws. Most are sit-and-wait predators of open or semi-open habitats that scan the surrounding area from a perch and take most prey from the ground. Larger prey items are often impaled or wedged for short-term storage. Insects usually dominate shrike diets, but all species probably take some vertebrates and they form a significant component of the diet in the larger species (Harris & Franklin, 2000). The most frequent vertebrate prey items mentioned for Oriental species—although not necessarily in the Region—are frogs, lizards, young birds and small rodents (LeFranc & Worfolk, 1997; Harris & Franklin, 2000). In Taiwan, small invertebrates dominated the diet of wintering *L. cristatus*, but frogs and lizards were most often impaled (Severinghaus & Liang, 1995). *L. cristatus* was the only significant avian predator on small vertebrates in winter in many suburban areas, where no raptors were present. Mohan (1994) saw *L. schach* feeding a 25-cm snake to a fledgling cuckoo.

Corvidae. **–** Small vertebrates have been reported as a component of the diet of Oriental corvids in the genera *Corvus*, *Dendrocitta*, *Garrulus*, *Pica*, *Platysmurus* and *Urocissa* (Roberts, 1992; Madge & Burn, 1994; Smythies & Davison, 1999). Bird eggs and nestlings are most frequently mentioned, followed by frogs, lizards, rodents and small birds.

Other passerines. **–** There are scattered reports of small vertebrates in the diets of many larger passerines, including broadbills (Eurylaimidae: Bruce, 2003), pittas (Pittidae: Erritzoe, 2003), orioles (Oriolidae: Smythies & Davison, 1999), drongos (Dicruridae: Roberts, 1992; Smythies & Davison, 1999), thrushes (Turdidae: Roberts, 1992; Smythies & Davison, 1999), starlings (*Gracula religiosa*, Sturnidae: Smythies & Davison, 1999), and babblers (*Turdoides striatus*, Timaliidae: Roberts, 1992).

MAMMALS

Insectivora

Although members of this order feed largely on invertebrates, many species are known to kill and eat any small vertebrates they are able to overcome (Nowak, 1999). Most Oriental records refer to the house shrew, *Suncus murinus* (Soricidae), which has been recorded as killing and eating frogs, snakes and small rodents in the wild (Phillips, 1980; Sharma, 1991b; Mandal, 1999), sparrow-sized birds in an aviary (Romer, 1963), and rats twice its own weight in captivity (Balakrishnan & Alexander, 1979). Small vertebrates also form part of the diet of the Region's gymnures and hedgehogs (Erinaceidae) (Sharma, 1991b; Nowak, 1999; Francis, 2008). Kloss's mole consumes some small vertebrates, including snakes and lizards (Kawada et al., 2003; Francis, 2008).

Chiroptera

All Oriental records of terrestrial vertebrate prey refer to the widespread false vampire bat *Megaderma lyra* (40–60 g) (Megadermatidae). In addition to large invertebrates, this species consumes fish, frogs, lizards, small birds (including *Zosterops*, *Nectarinia*, *Hirundo* and *Passer*), rodents, shrews and other bats (Lekagul & McNeely, 1988; Audet et al., 1991; Bates & Harrison, 1997; Nowak, 1999; Ramanujam & Verzhutskii, 2004b).

Scandentia

Small vertebrates, such as geckoes, form a minor part of the diet of several species of tree shrew (Tupaiidae) (Lim, 1967; Lekagul & McNeely, 1988; Nowak, 1999; Emmons, 2000), and captive *T. palawanensis* killed and ate lizards, small birds and mice (Dans, 1993).

Primates

There are scattered records of vertebrate predation, mostly of lizards, by tarsiers (*Tarsius* spp; Tarsiidae) and lorises (*Loris*, *Nycticebus*; Loridae) (Nowak, 1999). There have also been many observations of free-living macaques (*Macaca* spp.; Cercopithecinae) opportunistically capturing and eating lizards and frogs and, less commonly, birds and small mammals up to the size of a subadult Indian giant squirrel (*Ratufa indica*) (e.g. Estrada et al., 1978; Suzuki et al., 1990; Umapathy & Prabhakar, 1996; Hanya, 2004; Sushma & Singh, 2008). On Langkawi Island, *M. fascicularis* was seen to kill and eat colugos (Irshad Mobarak in Lim, 2007). Black crested gibbons (*Nomascus concolor*) in Central Yunnan killed and ate four juvenile giant flying squirrels (*Petaurista philippensis*) and attacked several adults (Fan & Jiang, 2009). However, among Oriental primates, only orangutans (*Pongo pygmaeus*; Hominidae) appear to systematically forage for vertebrates, in this case slow lorises (*Nycticebus coucang*) hiding in dense tangles of vegetation, with this behaviour known only from two sites in northern Sumatra, where some individuals apparently specialise on this tactic (van Schaik et al., 2003; van Schaik, 2004).

Carnivora

***Felidae*. –** The cats are hypercarnivores, requiring a higher proportion of protein in their diets than most other mammals (Sunquist & Sunquist, 2009) and apparently unable to detect the sweetness of carbohydrates (Li et al., 2005). They are highly specialised for killing live prey, with none of the morphological compromises required by the more omnivorous diet of many other Carnivora. Hypercarnivory is associated with specialisation of the teeth for slicing, rather than crushing, along with other shared features of the skull and dentition that we recognise as "cat-like", although other groups of carnivores have occupied this niche in the past (Van Valkenburgh, 1988). Oriental felids range in size from the 1-kg rusty-spotted cat (*Felis rubiginosus*) to the 75–260-kg tiger (*Panthera tigris*) and the similar sized, but much more restricted, lion (*Panthera leo*). Note that generic assignments in much of the regional literature do not reflect the current understanding of their relationships (Agnarsson et al., 2010).

The five largest extant Oriental felids, the tiger (*Panthera tigris*), lion (*P. leo*), leopard (*P. pardus*), snow leopard (*P. uncia*) and clouded leopards (*Neofelis* spp.), together with the New World jaguar (*P. onca*), form a well-supported monophyletic group (Johnson et al., 2006). The tiger and leopard were historically almost ubiquitous, while the lion was confined to northwest India, the clouded leopard to the eastern half of the Region, and the snow leopard to the northern margins of the Region, mostly above the treeline (Sunquist & Sunquist, 2009).

Siberian tigers are the largest living felids, but tropical tigers are similar in size to African lions, with adult males 100–260 kg and adult females 75–160 kg in the Region (Sunquist & Sunquist, 2009). Tigers from the Sunda shelf islands (Sumatra and, until recently, Java and Bali) are considerably smaller than those from northern India and southern China. Tigers occupied a variety of more or less wooded habitats throughout the Region, except on the islands of Sulawesi and the Philippines, and Borneo, where they may have survived into the last millennium (Cranbrook, 2010). Primary lowland rainforests appear to be a relatively unfavourable habitat for tigers, with very low population densities compared with habitats where a higher primary productivity at ground level supports a higher density of potential prey (Kawanishi & Sunquist, 2004). The tiger is the most specialised felid and densities at diverse sites are predicted fairly accurately by the densities of the ungulate prey on which they depend (Karanth et al., 2004; Kawanishi & Sunquist, 2004). Tigers select large prey, with mean prey weights above 50 kg at most sites and prey >100 kg forming an important component of the diet wherever available (Biswas & Sankar, 2002; Bagchi et al., 2003; Joseph & Thomas, 2006; Andheria et al., 2007; Avinandan et al., 2008; Sunquist & Sunquist, 2009). Deer—particularly *Axis axis* (70 kg) and *Rusa (Cervus) unicolor* (180 kg)—and wild pigs (<120 kg) were the major prey at most study sites, but they also prey regularly on gaur *Bos frontalis* (450–900 kg), where it is available, as well as a huge range of other species, from frogs, birds and fish to sun bears and the calves of elephants and rhinos. Adult elephants and rhinoceroses escape predation by tigers, and tapirs (395 kg) seem to be avoided for unknown reasons (Kawanishi & Sunquist, 2004). Tigers kill more people than any other carnivore in the Region. The predictive model of Karanth et al. (2004) assumes that each tiger consumes around 50 ungulates a year, representing 10% of all available prey. In general, tiger populations do not appear to survive for long in the absence of large prey, but the major prey species were <50 kg in Srisailam Tiger Reserve in southern India (Reddy et al., 2004) and were <20 kg *Muntiacus muntjak* in the Huai Kha Khaeng Wildlife Sanctuary in Thailand (Rabinowitz, 1989).

Through most of their range, tigers coexist with leopards and the dhole (*Cuon alpinus*). Tigers are socially dominant and sometimes kill leopards, but large dhole packs have been known to chase and, occasionally, kill tigers. There is considerable overlap in the types of prey taken by the three species, but dholes are strictly diurnal, while tigers are mostly crepuscular or nocturnal, and leopards take a wider range of generally smaller prey (Joseph & Thomas, 2006; Andheria et al., 2007; Ahmed & Khan, 2008; Wang & Macdonald, 2009; Sunquist & Sunquist, 2009). The historical range of tigers also overlapped in the west of the Region with that of the Asian subspecies of lion, *Panthera leo persica*. Lions prefer more open habitats than tigers, but both can utilise the mosaic of grassland and open forest which supports the highest ungulate biomass in Asia. Individual male lions have apparently killed tigers in captivity (according to a range of uncheckable Internet sources), and male lions in South Africa regularly take prey more than three times their own weight (Radloff & Du Toit, 2004), which tigers do not. Moreover, unlike all other wild felids, lions normally hunt in groups (1–15, with a mean of three in Asian lions (Singh 1995)),

which must make them the most formidable predators in the Region. African lions weigh 85–225 kg but there appear to be no reliable weights for the Asian subspecies. They are now confined to dry deciduous forest in and around the Gir National Park in northwest India, where the last 400 or so individuals prey largely on adults of *Axis axis*, *Rusa unicolor*, *Boselaphus tragocamelus* (120–240 kg), wild pigs, and domestic cattle and buffalo (Meena et al., 2011).

The most widespread felid, the leopard (29–70 kg in Asia), was absent only from Sumatra, Borneo, Sulawesi and the Philippines, as well as true deserts and alpine areas on the mainland. Not surprisingly for a species with such a wide geographic and environmental range, and which must compete almost everywhere with one larger felid and several smaller ones, adaptability is its most striking characteristic. Oriental leopards hunt mostly on the ground, eating whatever they can catch, but they climb well and monkeys are important prey, particularly where ungulates are rare (Joseph & Thomas, 2006; Sunquist & Sunquist, 2009; Wang & Macdonald, 2009). Most prey weigh 5–45 kg, including juveniles of larger species, but they can apparently kill much larger animals (c. <200 kg) and can survive on smaller prey (Arivazhagan et al., 2005; Odden & Wegge, 2009). In Africa, the preferred prey mass is c. 25 kg (Hayward et al., 2006). Leopards readily eat carrion and it is not always clear whether large species recorded in scats were killed or not. In Sanjay Gandhi National Park, on the edge of Mumbai, dogs and rodents were the commonest items in scats (Edgaonkar & Chellam, 2002).

The snow leopard is confined to high mountains from Pakistan to China. Slightly smaller than the leopard (22–52 kg), it is a rock specialist, living mostly above the treeline, but it moves lower in winter and in some regions year round (Sunquist & Sunquist, 2009). Over much of its range, the blue sheep or bharal, *Pseudois nayaur* (45 kg), is the most important prey, along with the ibex, *Capra siberica* (130 kg), Himalayan tahr, *Hemitragus jemlahicus* (130–180 kg), other ungulates, domestic stock (including 250-kg horses, yaks and cattle), and smaller animals, such as marmots, hares and pheasants (Gao, 1987; Sunquist & Sunquist, 2002; Bagchi & Mishra, 2006; Lovari et al., 2009). They reportedly chase prey further than other big cats.

The clouded leopards are considerably smaller (10-25 kg) than the other members of this group and are also the species about which least is known. Two species are currently recognised: *N. nebulosa* in mainland Southeast Asia and South China and *N. diardi* on the islands of Borneo and Sumatra (Sunquist & Sunquist, 2009). Both are largely confined to dense evergreen forests. The relatively small size, long tail, short legs and broad paws have been considered adaptations to an arboreal life. Most sightings have been on the ground, but recorded prey includes arboreal squirrels, slow lorises, macaques, leaf monkeys, proboscis monkeys and orangutans, as well as a range of medium-sized terrestrial species, such as hog deer (35 kg), muntjac (<25 kg), mouse deer, pigs, pangolins and civets (Grassman et al., 2005a; Matsuda et al., 2008; Sunquist & Sunquist, 2009). Clouded leopards have the largest canine teeth in relation to body size of any living felid and the widest maximum gape angle (c. 85°), but the significance of this is unknown.

The Asiatic golden cat, *Catopuma temminckii* (8–16 kg), occurs through much of the eastern Oriental Region, from northeast India to southern China and south to Sumatra, but not Borneo (Sunquist & Sunquist, 2002). The smaller but otherwise similar bay cat, *C. badia* (2–4 kg), occurs only on Borneo, where it appears to be widespread but rare (Kitchener et al., 2004). Very little is known about the ecology of the golden cat, despite its wide range, and nothing at all about the bay cat. Golden cats appear to be mostly terrestrial, although they climb well. Two adults radio-tracked in Thailand ranged over 33–48 km^2 (Grassman et al., 2005a) and both this study and a camera-trapping study in Malaysia (Mohd. Azlan & Sharma, 2006) showed no clear diurnal pattern of activity. The diet includes a variety of small vertebrates up to the size of mouse deer and the dusky leaf monkey (*Trachypithecus obscurus*), although there are reports of larger prey, including domestic sheep, goats and water buffalo calves (Gao, 1987; Lim, 2002; Sunquist & Sunquist, 2009). The marbled cat (*Pardofelis marmorata*) (2–5 kg) has a wide distribution in closed forests from northeast India to southwest China, and south to Borneo and Sumatra, but very little is known about its ecology. The big feet and very long tail, and its behaviour in captivity, are consistent with the marbled cat being more arboreal than most other Oriental felids. Activity seems to be largely nocturnal and crepuscular (Grassman et al., 2005a). Scattered reports on its diet mention rats, birds and squirrels (Sunquist & Sunquist, 2009).

The caracal (*Caracal caracal*) had a similar historical range to the cheetah, but is now rare in Pakistan and on the verge of extinction in India (Sunquist & Sunquist, 2002). It is a slender, long-legged cat that can sprint short distances at high speed and jump 2 m into the air from a standing start to catch a bird. Over the whole geographical range, body weights are 6–20 kg (Sunquist & Sunquist, 2009), but Indian caracals are apparently much smaller than those from Africa and the Middle East, at around 6 kg (Mukherjee et al., 2004). In the Region it inhabited a range of habitats from semi-desert to open dry forest. Caracals hunt mainly at night on the ground, but also climb well. Sunquist & Sunquist (2002) suggest they are "gazelle cats", specialised to hunt the 15–30 kg gazelles found throughout their historical range, but smaller prey dominates recorded diets. In Rajasthan, west India, 84% of scats (n = 25) had rodent remains, 36% birds, 20% reptiles and 40% invertebrates (Mukherjee et al., 2004). Each caracal was estimated to eat 8–9 rodents (each weighing 16–77 g) per day. Caracals, like cheetahs, were kept by Indian princes for hunting, and were apparently trained to hunt terrestrial prey up to the size of the barasingha (*Cervus duvauceli*, 145 kg) and nilgai (*Boselaphus tragocamelus*, 170 kg), as well as arboreal squirrels (Divyabhanusinh, 2002).

As well as being the only carnivore species lost from the Region in historical times, the cheetah, *Acinonyx jubatus*, a member of the otherwise American puma lineage, is isolated phylogenetically, morphologically and ecologically from

other Oriental felids. It is a largely diurnal predator that catches most of its prey in short, very high-speed chases (<102 km hr^{-1} in Africa) (Sunquist & Sunquist, 2009). Approximately the same weight as a leopard (22–65 kg in Africa), it is taller, slimmer and morphologically specialised for running, with an elbow joint more similar to a canid or hyena than other felids (Andersson, 2004). Cheetahs use the claw of the first digit of the front paw to hook fleeing prey off balance, in contrast to other large felids that knock the prey off balance (Londei, 2000). Four hundred years ago, cheetahs were common in open and semi-open habitats in central and western India, but the last known Indian cheetahs were shot in 1947 (Sunquist & Sunquist, 2002). The subspecies still survives in Iran. Their major prey seems to have been the blackbuck, *Antilope cervicapra* (38 kg), and most other recorded prey are in a similar size range (e.g., Jebeer gazelle (*Gazella bennettii*), wild sheep, *Ovis orientalis*, and Persian ibex, *Capra aegagrus*, in central Iran; Farhadinia & Hemami, 2010). Indian princes used trained cheetahs to hunt and even imported African ones when they became scarce in India (Divyabhanusinh, 2002).

The jungle cat, *Felis chaus*, is the largest (3–12 kg) and most widespread of this genus in the Region, ranging from Pakistan to Sri Lanka and southwest China, but not Malaysia or Indonesia (Sunquist & Sunquist, 2009). Despite its name, this species is not usually found in dense forest, preferring grasslands, open forests and cultivated areas, often, but not always, near water. It hunts mostly on the ground and is often seen during the day. One was clocked at 32 km hr^{1} from a car (Roberts, 2005). Most reported prey is <1 kg, although they occasionally kill larger prey such as juvenile ungulates. A study in Rajasthan, western India, found that 73% of 69 scats contained the remains of rodents, 42% birds, 26% reptiles and 23% invertebrates (Mukherjee et al., 2004). Each cat was estimated to eat 3–5 rodents (weighing 16–77 g) a day. Most scats in cultivated areas in Pakistan were also dominated by rodents (Khan & Beg, 1986). Fish and frogs are eaten elsewhere.

The Asian form of the wild cat, *Felis silvestris* (3–4 kg), enters the Region only in Pakistan and northwest India, where it is associated mostly with semi-desert habitats (Sunquist & Sunquist, 2009). It is largely terrestrial and nocturnal, feeding mostly on rodents, but also taking occasional larger prey (<3–4 kg) such as young ungulates, as well as birds, reptiles and invertebrates. It hybridises freely with the closely related domestic cat. The sand cat, *F. margarita* (2–3 kg), has an even more restricted range within the Region, occurring only in sandy deserts in western Pakistan (Roberts, 2005). It is a desert specialist, in terms of its morphology and physiology, its highly developed hearing, and its opportunistic diet, including small mammals, birds, reptiles and invertebrates.

Free-ranging domestic cats, *Felis catus*, occur in and around most human settlements in the Region, but the distribution and abundance of genuinely feral populations have not been investigated. Cats were domesticated later than dogs and most still supplement their diet by hunting, so one would expect the domestic-feral transition to be relatively easier. Feral cats on Iriomote Island (24°N) were associated with garbage dumps, but also preyed on rats, birds, frogs and invertebrates (Watanabe et al., 2003). On nearby Okinawa (27°N), 11 feral cat scats contained the remains of birds, shrews, snakes, frogs and invertebrates (Kawauchi & Sasaki, 2002). On Hahajima (26°N), in the Bonin Islands, feral cats apparently prey on seabirds, particularly the wedge-tailed shearwater (*Puffinus pacificus*), as well as rats (Kawakami & Fujita, 2004), while a free-ranging domestic cat concentrated on small birds, particularly the introduced *Zosterops japonicus* (Kawakami & Higuchi, 2002). Elsewhere in the Region, feral cats prey on both egg-laying megapodes and newly emerged chicks on the Moluccan island of Haruka (Heij, 2001). Feral cats have been responsible for a large percentage of global vertebrate extinctions, particularly on islands (Nogales et al., 2004), so more work is clearly needed on the potential threat posed by this species in the Region. Domestic cats are assumed to have less impact per cat (Kays & DeWan, 2004), but can live at unnaturally high densities and in areas that cannot support feral cat populations.

The leopard cat, *Prionailurus bengalensis* (1–4 kg), has the widest Oriental distribution of any small felid and is absent only from the extreme west and from the Philippines and Sulawesi (Sunquist & Sunquist, 2002). Like all members of this genus, leopard cats are excellent swimmers and the species occurs on many offshore islands (Watanabe, 2009). A distinctive subspecies, *P. bengalensis iriomotensis*, occurs on the southern Ryukyu island of Iriomote (24°N). Leopard cats occupy a wide range of mostly forested habitats, but also seem to survive in deforested, human-dominated landscapes better than most other Asian felids. Although usually considered to be nocturnal, radio-telemetry and camera-trapping studies have found them to also be active during the day (Rabinowitz, 1990; Grassman et al., 2005b; Mohd. Azlan & Sharma, 2006). Rats and mice dominate the diet in most studies, but they have also been reported to take a wide variety of other small vertebrates, including squirrels, tree shrews, hares, mouse deer (*Tragulus javanicus*, 3 kg), birds, lizards, snakes, frogs and fish (Gao, 1987; Rabinowitz, 1990; Khan, 2004; Grassman et al., 2005b; Austin et al,. 2007; Rajaratnam et al., 2007; Sunquist & Sunquist, 2009). Gao (1987) says they will attack *Muntiacus.* The well-studied Iriomote subspecies (3–5 kg) has an extremely broad diet, including rats, the Ryukyu flying fox, birds, skinks, snakes, frogs and invertebrates (Nowell & Jackson, 1996; Izawa et al., 2000).

The fishing cat (*Prionailurus viverrinus*) and the flat-headed cat (*P. planiceps*) have a lot in common (Nowell & Jackson, 1996; Sunquist & Sunquist, 2009). Both have an elongated head, short legs and a very short tail, contributing to their rather un-catlike appearances, with the fishing cat most often compared to a civet (hence "*viverrinus*") and the flat-headed cat to a mustelid. Both are associated largely with wetlands, both take to water readily, and both prey heavily on fish. Both species use their forepaws to search for prey underwater (Iwaniuk et al., 2001). The flat-headed cat, however, is much more specialised as a fish-eater, with its more completely webbed toes and a long and pointed

second upper pre-molar, which enables it to grasp slippery prey. Other peculiar features of this small (1.5–2.5 kg) cat, including its flattened head, large close-set eyes, and small ears, may also be adaptations to its semi-aquatic existence. The little information on its natural diet shows it to be dominated by fish, plus other aquatic animals, including frogs and crustacea, although flat-headed cats have been known to prey on poultry. It is confined to peninsular Thailand, the Malay Peninsula, Sumatra and Borneo. The fishing cat, in contrast, is a larger (5–16 kg), less specialised cat, with a wider but discontinuous distribution that includes parts of Pakistan, Sri Lanka, southwest and northeast India, Nepal, Bangladesh, and Southeast Asia to Sumatra and Java, but not Borneo or the Malay Peninsula. Fish appear to be its most frequent prey at most sites, but it is also known to take birds, rodents, a small Indian civet (*Viverricula indica*), snakes, other reptiles, frogs and a variety of domestic animals, including dogs (Sunquist & Sunquist, 2009).

The rusty spotted cat, *Prionailurus rubiginosus*, may be the smallest cat species, at 1.0–1.6 kg (Sunquist & Sunquist, 2009). It is found in Sri Lanka and much of peninsular India, but little is known about its ecology. It occurs in a range of habitats from grassland to dense forest, is mostly nocturnal, and seems to hunt mostly on the ground, consuming a variety of small vertebrates.

***Prionodontidae*. –** The Asian linsangs (two species of *Prionodon*) have traditionally been included among the civets, but molecular data strongly support family status (Agnarsson et al., 2010). This is consistent with their cat-like appearance and behaviour, retractile claws, and hypercarnivorous dentition, as well as their largely carnivorous diet. Both species are smaller than any cat or Oriental civet, with the banded linsang (*P. linsang*) weighing 600–800 g and the spotted linsang (*P. pardicolor*) around 600–1200 g (Gaubert, 2009). The spotted linsang occurs in hill forests from Nepal and northeast India, through northern Myanmar and Thailand, to Laos, Vietnam and southwest China, while the banded linsang occurs in forests from southern Myanmar and Thailand to Sumatra, Borneo and Java. Both species appear to be equally at home in trees and on the ground and are reported to feed on rats, squirrels, birds, lizards, snakes, frogs and insects (Gao, 1987; Van Rompaey, 1993; Shrestha, 1997; Nowak, 1999; Gaubert, 2009). Like cats but unlike most civets, they do not seem to eat fruit.

***Hyaenidae*. –** Hyenas are characterised by a bone-cracking dentition, with relatively wide premolars (Van Valkenburgh, 1988). The striped hyena (*Hyaena hyaena*), was widespread in suitable habitats from Pakistan to Nepal and Bangladesh, and south through India to the Nilgiri Hills (Gurung & Singh, 1996). The bone-cracking niche is currently unoccupied in the east of the Region and in densely forested areas of the west, presumably because large carcasses are too rare or too difficult to locate in closed forest. However, the spotted hyena (*Crocuta crocuta*; 45–80 kg) survived in southern China until at least the Late Pleistocene and a giant hyena (*Pachycrocuta brevirostris*; >100 kg) was present in non-forest habitats in the Region earlier in the Pleistocene (Corlett, 2010). Oriental hyenas weigh 30–50 kg and occur in a wide range of more or less open habitats, where they are usually solitary foragers (Prater, 1980; Shreshta, 1997; Roberts, 1997; Nowak, 1999). They seem to live largely as scavengers and their ability to crush the largest bones enables them to exploit carcasses already picked clean by vultures (Roberts, 1997). There are also reports of striped hyenas appropriating kills from leopards (Prater, 1980; Roberts, 1997). However, striped hyenas also kill a variety of small and medium-sized mammals, including domestic sheep, goats and dogs, and the occasional human child. They are also known to eat tortoises and considerable quantities of fruit. Twenty-six hyena scats collected in Rajasthan, northwest India, contained the remains of *Axis axis* (35% of scats), *Boselaphus tragocamelus* (14%), domestic cattle (17%) and goats (14%), and hares, *Lepus nigricollis* (7%), as well as fruit, a bird and a rodent, but it was not possible to distinguish predation from scavenging (Sankar & Jethwa, 2002).

***Herpestidae*. –** Almost every habitat in the Region supports at least one (<3) species of mongoose (*Herpestes*). All eight or so Asian mongoose species have long, slender bodies, short legs with non-retractile claws, a tapering snout, small rounded ears and a long tail. The smallest species, such as *H. javanicus*, weigh <1.2 kg while the largest (*H. urva* and *H. vitticollis*) can weigh >3 kg (Prater, 1980; Lekagul & McNeely, 1988; Roberts, 1997). All are predominantly terrestrial, but some species climb trees and some are strongly associated with water. Most species appear to be largely diurnal, although literature reports are not consistent on this. All species are usually solitary foragers and, although pairs are sometimes reported, there is no evidence of cooperative hunting.

Asian mongooses are opportunistic predators of large invertebrates and small vertebrates, but there have been no detailed studies of the diet of wild populations within their native range. Invertebrates are the most frequent items in scats, but small vertebrates are probably more important for most species in terms of biomass consumed (e.g. Gorman, 1975; Abe et al., 1999). *Herpestes javanicus* (often called *H. auropunctatus*) is by far the best-studied species, but almost entirely in areas where it has been introduced to control rats or snakes outside its native range, often with disastrous consequences for endemic vertebrates (Roy, 2002; Quinn & Whisson, 2005). One such well-studied introduction was to Amami Island (28°N), on the northeast fringes of the Region, where 30 individuals were released in 1979 (Abe et al., 1999; Yamada, 2002; Watari et al., 2008). On this island, the vertebrate component of the diet includes mammals (particularly *Rattus tanezumi*), birds, frogs and reptiles, but very rarely the snake (*Protobothrops flavoviridis*) it was intended to control. Eight percent of scats contained remains of the endangered endemic rabbit, *Pentalagus furnessi*, which has an adult weight of 2–3 kg. Generally similar diets have been reported for other introduced and native populations of this species (Gorman, 1975; Prater, 1980; Gao, 1987; Lekagul & McNeely, 1988; Roberts, 1997; Ogura et al., 2002).

Scattered information for the other species suggests that they share broadly similar diets as well as an ability to kill

prey larger than themselves (Phillips, 1980; Prater, 1980; Lekagul & McNeely, 1988; Roberts, 1997). An ability to kill highly venomous snakes has also been widely reported, particularly for *H. edwardsi*, and seems to reflect their speed and agility together with a relative resistance to both hemorrhagic and neurotoxic venoms (Dunham, 2003). One of the two largest species, *H. vitticollis*, has been reported to prey on hares (*Lepus nigricollis*, 2–6 kg) and mouse deer (*Tragulus meminna*, 3–4 kg) (Phillips, 1980; Van Rompaey & Jayakumar, 2003). The diet of the other large species, *H. urva*, is dominated by aquatic vertebrates and invertebrates, according to most accounts (Lekagul & McNeely, 1988; Chuang & Lee, 1997; Van Rompaey, 2001), but Wang (1999) found that the remains of rodents and snakes were common in scats from southern China.

***Viverridae*. –** After the exclusion of the linsangs, most Asian civets fall into three groups—true civets (Viverrinae), palm civets (Paradoxurinae) and the rest (Hemigalinae). Most Asian civets are omnivores, consuming vertebrates, invertebrates and plant foods, particularly fruits (Corlett, 1998; Jennings & Veron, 2009). This is reflected in their dentition, which is much less specialised than that of the felids. The vertebrate prey of civets is generally small in comparison with felids of similar body mass. As many as six civet species can coexist in the same area (e.g. Mohd. Azlan, 2006).

The four Oriental species of Viverrinae are nocturnal, terrestrial (at least when foraging), solitary omnivores. The smallest and most widespread species, *Viverricula indica* (2–4 kg), occupies almost all habitat types, from rainforest to semi-desert, but appears to be most common in non-forest or partly forested habitats, often near human habitations. Reported diets include varying proportions of small vertebrates (rodents, shrews, birds and reptiles), invertebrates and fruit (Prater, 1980; Gao, 1987; Lekagul & McNeely, 1988; Roberts, 1997; Chuang & Lee, 1997; Wang & Fuller, 2003a; Jennings & Veron, 2009). The three *Viverra* species are larger (3–11 kg), but have essentially similar diets, with rodents the most consistent component (Wemmer & Watling, 1986; Gao, 1987; Lekagul & McNeely, 1988; Auffenberg, 1988; Lim, 1991; Colón, 1999; Jennings & Veron, 2009). Jha (1999) says that *V. zibetha* in India hunts prey larger than itself, including dogs, goats, deer and even buffalo calves, but I can find no other support for this statement.

The Paradoxurinae are largely nocturnal and generally more arboreal and more frugivorous than the Viverrinae. The most widespread species, *Paradoxurus hermaphroditus* (2–5 kg), is largely arboreal in forest, but has adapted to life in human-made structures in and around human settlements (Lekagul & McNeely, 1988; Krishnakumar & Balakrishnan, 2003). It appears to prefer fruit when this is available, but can live on invertebrates or small vertebrates (mammals, birds and reptiles) when fruit is rare (Gao, 1987; Auffenberg, 1988; Joshi et al., 1995). The other three species of *Paradoxurus* are largely arboreal, forest frugivores, but *P. lignicolor*, endemic to the Mentawai Islands, is reported to prey on village chickens (Abegg, 2003). *Paguma larvata* (3–5 kg) is less arboreal and less exclusively nocturnal than *Paradoxurus*, but has a similar diet, at least seasonally dominated by fruit, and also thrives near human settlements in some areas (Gao, 1987; Lekagul & McNeely, 1998; Wang & Fuller, 2001, 2003a; Dudgeon & Corlett, 2004).

Macrogalidia musschenbroeki is the only native species in the order Carnivora on Sulawesi, although two other viverrids have been introduced. It inhabits forests from the lowlands to the montane zone, but also takes poultry from villages (Wemmer & Watling, 1986). Although a skilful climber, it probably feeds mostly on the ground. Its diet is apparently dominated by fruits, especially palm fruits, but it also eats rodents, the nocturnal dwarf cuscus (*Strigocuscus celebensis*), and birds, and local people say it takes piglets of *Sus celebensis* and, occasionally, domestic pigs. The binturong, *Arctictis binturong*, is a large (9–20 kg) arboreal species of dense Southeast Asian forests, with slow and deliberate movements. It and the Neotropical kinkajou (*Potos*) are the only Carnivora with truly prehensile tails. Very little is known of its diet but it appears to be largely frugivorous. *Arctogalidia trivirgata* (2–2.5 kg) is morphologically distinct and its relationships require further study (Agnarrson et al., 2010). It is a nocturnal, arboreal species of forest canopies in Southeast Asia, which is reported to feed on squirrels, birds, frogs, insects and fruits, although no quantitative dietary information is available (Lekagul & McNeely, 1988; Jennings & Veron, 2009).

The Hemigalinae includes four distinctive-looking civets of Southeast Asian forests, all of which seem to feed largely on invertebrates, although vertebrate prey may be taken occasionally (Nowak, 1999): *Hemigalus derbyanus* (1–3 kg), *Diplogale hosei* (1.4 kg), *Chrotogale owstoni* (2–3.5 kg) and the otter civets, *Cynogale bennettii* (4 kg).

***Canidae*. –** Most canids are adapted to relatively open habitats, so most species are confined to the west and north of the Region. The Oriental dogs span the full range of variation found in the family, from solitary omnivores to pack-hunting predators of animals considerably larger than themselves.

Two similar-sized pack-hunting taxa, the dhole (*Cuon alpinus*) and the wolf (*Canis lupus*, in the broad sense) effectively partitioned the Region in the past, although they coexist in habitat mosaics today. Oriental dholes occupy most of the forested parts of India and southern China, south through Southeast Asia to Sumatra and Java. Males are 15–20 kg, females 10–12 kg and reported pack size averages around 3–12 adults, with an extreme of 40 (Cohen, 1978; Gao, 1987; Indrawan et al., 1996; Karanth & Sunquist, 2000; Silbero-Zubiri, 2009). Dholes are diurnal hunters and are most active in the early morning and evening. They specialise on hunting whatever ungulates are locally available, but are also reported to take hares, rodents and other small vertebrates at some sites (Cohen et al., 1978; Prater, 1980; Barnett et al., 1981; Fox, 1984; Gao, 1987; Venkataraman et al., 1995; Indrawan et al., 1996; Wang, 1999; Karanth & Sunquist, 2000; Austin, 2002; Grassman et al., 2005c; Joseph & Thomas, 2006; Silbero-Zubiri, 2009). Unlike wolves, dholes rarely attack

domestic stock, although they are reported to take goats in Kerala (Veermani et al., 1996) and sheep in Bhutan (Wang & Macdonald, 2009). Most chases do not last long (<500 m). Most prey in India is <50 kg, but dholes regularly kill adult male *Axis axis* (75 kg) and *Rusa unicolor*, including adult males (>200 kg), is the major prey species at some sites (Austin, 2002; Kumara et al., 2004; Grassman et al., 2005c; Joseph & Thomas, 2006; Borah et al., 2009). Dholes in Java kill adult female *Rusa timorensis* (95 kg) and sub-adult or female *Bos javanicus* (<500 kg), the latter in packs of 9-23 individuals (Indrawan et al., 1996). Conversely, the small (< 4) packs of dhole at a rainforest site in Peninsula Malaysia preyed mostly on mouse deer (2–4.5 kg) (Kawanishi & Sunquist, 2008). Large prey usually dies from shock or loss of blood as a result of multiple injuries. Jog et al. (2005) found that the density of sarcocysts of the protozoan parasite *Sarcocystis* in the heart muscles of dhole-killed *Axis axis* was significantly higher than in animals that died of other causes, suggesting that dholes select infected prey and, since the dhole is an obligatory host for the sexual cycle of the parasite, that the relationship between predator and parasite could be mutualistic. Dholes appear to have substantially larger area requirements for persistence in protected areas than do tigers, perhaps because their larger home ranges (70 km^2 for dholes vs. 17 km^2 for tigers in India) bring them more often into conflicts with people (Woodroffe & Ginsberg, 1998). Meat-stealing from dhole kills by local people is a problem in some areas (Kumara et al., 2004).

Wolves once occupied most habitats in the Region other than tropical forests and deserts. Recent mtDNA studies identified three distinct lineages of wolves: one confined to lowland India and Pakistan, one found at high elevations from eastern Nepal and Tibet to eastern Kashmir, and the "wolf-dog" clade that includes all other wolves in the Region, as well as those in the Palaearctic and Nearctic, and all domestic and feral dogs (Sharma et al., 2004; Aggarwal et al., 2007). Further studies are needed, but it is possible that these three lineages deserve recognition as separate species. Little is known about the ecology of the Himalayan wolf lineage, but there have been a number of studies of the lowland wolves (Jhala, 2003; Kumar & Rahmanai, 2008). Although male wolves from India and Pakistan can attain 24– 27 kg (Roberts, 1997; Prater 1980), most seem to be <20 kg, which is more similar to the dhole than to the wolves of the Palaearctic and Nearctic (Nowak, 1999). Centuries of persecution because of attacks on livestock and, less commonly, children (Shahi, 1982; Rajpurohit, 1999) have made it very difficult to reconstruct the natural predatory behaviour of lowland Indian wolves. Most wolves in human-dominated landscapes combine scavenging and predation on livestock (Shahi, 1982; Jhala, 2003; Singh & Kumara, 2006). Away from human settlements, Oriental wolves take a variety of wild ungulates, but also hares, rodents and other small vertebrates (Kumar & Rahmani, 2000, 2008; Jethva & Jhala, 2003; Jhala, 2003). Blackbucks (*Antelope cervicapra*) are the major prey in western India, with the wolves preferring old or injured adult males (c. 40 kg) (Kumar & Rahmani, 2008). Reported pack sizes are mostly 1–7, with a maximum of 12, and most kills are made at night, although this may be partly to avoid persecution. Most chases last less than 0.5 km (Jhala, 2003), but they can continue considereably longer (Kumar & Rahmani, 2008). Untill recently, lowland wolves would have competed with cheetahs in much of their range.

Domesticated dogs (*C. lupus familiaris*) appear to have originated from wolves by multiple independent domestication events and have probably been genetically separate from them for around 8000 years (Verginelli et al. 2005). Today, every possible intermediate from fully domesticated to fully feral dogs can be found in the Region, mostly near human settlements (Corbet & Hill, 1992; Irion et al., 2005; Vanak & Gompper, 2009, 2010). The diversity of size, shape and other characteristics declines along this gradient and most feral dogs in the Region have converged on (or retained?) a single, dingo-like form. Little is known about the ecology of feral and semi-feral dogs in the Region. Hunting behaviour was presumably selected against during domestication, because of the threat to people and other domesticates, but feral dogs sometimes hunt wild prey larger than themselves in small packs, as well as taking small vertebrates, carrion and garbage (Auffenberg, 1981; Jhala, 1993; Kawauchi & Sasaki, 2002; Manor & Saltz, 2004; Dudgeon & Corlett, 2004; Das et al., 2006; Vanak & Gompper, 2009).

The golden jackal (*Canis aureus*) looks like a small (7–12 kg) wolf. It occurs from Thailand and Myanmar westwards, mostly in relatively open habitats and often near human settlements. Rodents, carrion and a wide range of plant material are the most frequently recorded dietary items, along with other small mammals, ground birds and their eggs, reptiles, frogs, fish and invertebrates (Schaller, 1967; Prater, 1980; Khan & Beg, 1986; Sarker & Ameen, 1990; Roberts, 1997; Nowak, 1999; Jaeger et al., 2007; Silbero-Zubiri, 2009). They are mostly nocturnal and usually seen alone, although packs of 3–5 have also been reported. Pairs or larger groups may attack domestic goats, langurs (*Presbytis* spp.), small deer and the young of larger species (Stanford, 1989; D'Cunha, 1996; Silbero-Zubiri, 2009).

Foxes (*Vulpes* spp.) are small (1–10 kg), relatively short-legged canids that occupy most of the western part of the Region, as well as southern China and northern Vietnam, but are absent from the tropical forests of Southeast Asia. *V. bengalensis* (1.8–3.2 kg) occupies most of India, *V. vulpes* enters the northern part of the Region from Pakistan to South China, and the ranges of *V. cana* (c. 1 kg) and a desert specialist, *V. rueppelli* (1.5–3 kg), extend into the northwest of the Region. A highland species, *V. ferrilata* (3–5 kg), enters the northern margins of the Region in Nepal. Foxes live in pairs but are usually solitary hunters. Diets are usually dominated by rodents and other small mammals, but also include ground birds, reptiles, frogs, invertebrates and fruits (Prater, 1980; Roberts, 1997; Sharma, 1997; Nowak, 1999; Home & Jhala, 2009; Vanak & Gompper, 2009; Silbero-Zubiri, 2009).

The raccoon dog (*Nyctereutes procyonoides*) (4–8 kg) enters the northeast of the Region in southern China and northern Vietnam, where it inhabits a variety of forest types. It is a nocturnal omnivore, feeding on small mammals, birds,

reptiles, frogs, invertebrates and large amounts of fruit (Gao, 1987; Silbero-Zubiri, 2009).

***Ursidae*. –** Four bear species more or less partitioned the Region in historical times, although their distributions have now been greatly reduced. The sloth bear (*Melursus ursinus*) occupied Sri Lanka and most of the Indian subcontinent, except deserts and high mountains. The sun bear (*Helarctos malayanus*) occupied most of Southeast Asia, from southwest China south to Sumatra and Borneo. The Asiatic black bear (*U. thibetanus*) occupied forests in southern China and a belt across the Himalayan ranges west to Pakistan. The range of this species had a broad overlap with the sun bear in continental Southeast Asia and a narrower one with the sloth bear in northern India, with all three species apparently coexisting in parts of eastern India. Finally, the brown bear (*U. arctos*) occurs largely in alpine habitats on the margins of the Region in India and Pakistan.

The Oriental bears appear to feed largely on fruit and plant material, and on invertebrates, and most evidence for carnivory is anecdotal. However, all species are capable of killing an adult human. The Asiatic black bear (males 110–180 kg, females 59–90 kg) is largely vegetarian (Schaller, 1969; Gao, 1987; Reid et al., 1991; Roberts, 1997; Hwang, 2003; Sathyakumar & Viswanath, 2003), but they have been reported to dig *Alticola* voles out of their burrows (Johnsingh, 2003). They sometimes kill sheep and goats (Roberts, 1997) and, occasionally, larger domestic animals up to the size of an adult buffalo (Prater, 1980; Nowak, 1999). Presumably they also take wild vertebrates opportunistically (Hwang, 2003), like the related American black bears. Although brown bears (<400 kg) are relatively carnivorous in some parts of their huge natural range (e.g., Xu et al., 2006), the few Oriental reports suggest that they are largely herbivorous here (Prater, 1980; Roberts, 1997). Like black bears, they are reported to dig rodents out their burrows and some individual bears kill sheep, goats and other livestock.

The sun bear (27–65 kg) is the smallest and most arboreal bear. The long tongue and protrusible lips are presumably adaptations to insectivory, but they do not seem to maintain body condition on invertebrates alone and become almost totally frugivorous during mast fruiting periods (Wong et al, 2004; Fredriksson et al., 2006). They are also reported to kill small vertebrates, including tortoises, and, occasionally livestock, as well as scavenging on tiger kills (Wong et al., 2002; Ward & Kynaston, 1995; Nowak, 1999; Fitzgerald & Krausman, 2002; Wong et al., 2004). The sloth bear (males 80–150 kg, females 55–95 kg), is even more specialised as an insectivore, feeding largely on ants, termites and fruits in a wide range of habitat types (Garshelis et al., 1999; Sacco & Van Valkenburgh, 2004). Most studies have found no direct evidence of vertebrate consumption (e.g. Schaller, 1967; Laurie & Seidensticker, 1977; Gokula et al., 1995).

***Mustelidae*. –** There are around 23 species of mustelids in the Region, although several of these barely penetrate the northern margins. The family occurs throughout, except in the Philippines (excluding Palawan) and Sulawesi, but is represented only by otters on Sri Lanka. The two species of stink badger (*Mydaus*) are now placed in the skunk family, Mephitidae (Flynn et al., 2005). The diet of stink badgers is dominated by invertebrates, with some plant material, and there are no records of them taking vertebrates.

The weasels (*Mustela* spp.) are represented by nine species (three only marginally) that range from the Himalayan region to southern China and south to Sumatra, Borneo and Java, but the genus is absent from most of India (Corbet & Hill, 1992). The Oriental species are small (50–800 g), long-bodied, short-legged carnivores that are mostly terrestrial, diurnal or nocturnal. The little dietary information available from the Region suggests they feed mostly on rodents and other small vertebrates (Prater, 1980; Gao, 1987; Roberts, 1997, 2005; Jha, 1999; Nowak, 1999), but more detailed studies of *M. sibirica* in mainland China (Gao, 1987), on Taiwan (Wu, 1999), and on the southern Palaearctic island of Tsushima (Tatara & Doi, 1994), suggest that this species, at least, is an extreme opportunist, with the diet dominated by rodents, shrews, birds, frogs, invertebrates or fruits at different sites or seasons.

The marbled polecat (*Vormela peregusna*) (600 g) inhabits open, semi-arid areas in Pakistan, where it feeds on a variety of rodents and other small vertebrates (Roberts, 1997). It is mostly nocturnal and, although it can climb, it captures most of its prey on or under the ground. There are three species of martens (*Martes* spp.) in the Region, the widespread *M. flavigula*, *M. gwatkinsii* in southern India and *M. foina* on the northern fringes of the Region. *M. flavigula* and *M. gwatkinsii* are bigger than weasels (2–3.5 kg), largely diurnal or crepuscular, and have omnivorous diets. They hunt in trees and on the ground, sometimes in pairs or in larger, presumably family, groups (Prater, 1980; Gao, 1987; Ramakantha, 1994; Roberts, 1997, 2005; Nowak, 1999; Austin & Tewes, 1999; Madhukumar, 2002; Mudappa, 2002; Grassman et al., 2006; Larivière & Jennings, 2009). Their reported prey includes a wide variety of small vertebrates, up to the size of *Tragulus meminna* (2.5 kg) and juveniles of larger ungulates, plus some fruit and insects.

The ferret badgers (*Melogale* spp.), which are not closely related to the true badgers, are small (1–3 kg) nocturnal animals that feed largely on invertebrates, although small mammals, birds, reptiles and frogs are also occasionally eaten (Prater, 1980; Gao, 1987; Chuang & Lee, 1997; Nowak, 1999; Wu, 1999). The Asian badger (*Meles leucurus*) (3.5–9 kg) enters the northeast of the Region and presumably feeds on small vertebrates, invertebrates and fruit like its European relative (*M. meles*) (Larivière & Jennings, 2009). The hog badgers (*Arctonyx* spp.) (7–14 kg) occur from the eastern Himalayas to China and south to Thailand and Sumatra. Although usually reported to feed largely on invertebrates, 43 of 45 scats attributed to hog badgers in Jiangxi, China, contained the remains of rodents, and some contained hares, hedgehogs, birds or snakes (Wang, 1999; Wang & Fuller, 2003b). The ratel or honey badger (*Mellivora capensis*) (c. 9 kg) ranges from southern Africa to the drier parts of peninsular India. It is reported to feed on a variety of small

vertebrates, invertebrates and plant material in the Region (Prater, 1980; Roberts, 1997; Pati et al., 2001), but is known to kill larger prey in Africa (Larivière & Jennings, 2009).

The Region's otter species (*Aonyx cinerea*, *Lutra lutra*, *L. sumatrana*, *Lutrogale perspicillata*) feed primarily on aquatic prey, mostly at night, but all four species take terrestrial rodents and birds when the opportunity arises (Prater, 1980; Gao, 1987; Kruuk et al., 1994; Kanchanasaka, 1997; Roberts, 1997; Nowak, 1999; Lariviere, 2003; Anoop & Hussain, 2005). Prater (1980) says that *Lutrogale perspicillata* "takes to jungle hunting like other land carnivores" when pools and streams dry out.

***Ailuridae.* –** The red panda (*Ailurus fulgens*) feeds mostly on bamboo leaves, but it is also said to occasionally consume small rodents, young birds and bird eggs (Gao, 1987; Nowak, 1999).

Artiodactyla

An Oriental species, the wild boar (*Sus scrofa*, Suidae), is known to regularly consume a wide range of vertebrate prey, both within its native range in Europe and as a feral animal in the USA and Australia (Schley & Roper, 2003; Wilcox & Van Vuren, 2009). Reported prey includes mammals up to the size of rabbits, lambs and deer fawns, bird eggs and nestlings, amphibians and reptiles. At least part of this involves active predation, although they also scavenge on carcasses. One *Sus barbatus* scavenged an orangutan carcass in Borneo (Galdikas, 1978).

Rodentia

The rodents are the most diverse and abundant order of mammals in the Region, but all the evidence that they are significant predators on vertebrates comes from commensal species (largely *Rattus* spp. and *Mus musculus*) introduced to rodent-free islands, where they are associated with extinctions or declines of native rodents, bats, birds and reptiles (e.g. Towns et al., 2006).

DISCUSSION

***Diversity*. –** Mammals, birds and snakes are surveyed separately and few areas smaller than an entire country have checklists for all three. Even where survey effort is adequate, recent species lists from the Region rarely reflect habitat potential, because of the impacts of hunting over recent decades. The following summary of sympatric species richness therefore includes a variable amount of subjective interpretation with regards to the comprehensiveness of the surveys, the area and habitats surveyed, the validity of combining checklists for different groups from different areas, and the impacts of recent hunting. Generalisations are made easier, however, by the large geographical ranges and broad habitat tolerances of most carnivore species, which have resulted in considerable uniformity in historical carnivore faunas over large areas.

The Oriental Region supports a total of 80 species in the order Carnivora (Wilson & Reeder, 2005). The most intact mammalian communities in lowland tropical Asia support 15–25 species, with the greatest diversities at Southeast Asian sites with extensive closed-canopy forest (Rabinowitz & Walker, 1991; Lynam et al., 2005; Mohd. Azlan, 2006; Johnson et al., 2006; Grassman et al., 2004). Different forest sites support up to eight sympatric cats, six civets (plus *Prionodon*), three mongooses, eight mustelids (including otters), two canids and two bears (Rabinowitz & Walker, 1991, Johnsingh, 2001; Lim et al., 2003; Grassman et al., 2005; Lynam et al., 2005; Mohd. Azlan, 2006; Johnson et al., 2006; Grassman et al., 2004; Wilting et al., 2010). The diversity of Carnivora declines in more open habitats, with altitude, on small islands, in the subtropics (e.g. Zeng et al., 2005), and with habitat fragmentation and hunting pressure. The Region supports a total of 104 diurnal raptors (Accipitridae and Falconidae) and 70 owls (Strigidae and Tytonidae) (Inskipp et al., 1996). Forested sites typically support 10–12 diurnal raptors (Thiollay, 1998), with several additional species in edge and open habitats, and up to eight owls (Francis & Wells, 2003). The Region supports around 600–700 vertebrate-eating snake species. There are fewer reliable snake inventories, but forested sites in tropical Asia can support >20 species (Inger & Colwell, 1977; Luiselli, 2006). With the addition of the few carnivorous species outside the snakes, raptors and Carnivora, and the exclusion of those snakes that do not eat vertebrates and the largely vegetarian bears, this data suggests that a typical lowland forest site in tropical Asia can potentially support 45–65 vertebrate species that regularly feed on other vertebrates.

***Coexistence*. –** Greene (1988) noted that every feeding guild at La Selva, Costa Rica, contains members of each class of carnivores, but his guilds were very broadly defined, so that jaguars, boa constrictors, hawk-eagles and owls were grouped together. For the Oriental Region, while every class of prey is consumed by every class of predator, mammalian carnivores have exclusive access to the largest mammalian prey (Table 1). At the other end of the size spectrum, frogs, lizards and small mammals have such a wide range of potential predators that the evolution of predator-specific defences must be impossible.

In the absence of hunting, prey availability appears to be the main factor controlling carnivore densities, although there are exceptions to this (Creel et al., 2001; Carbone & Gittleman, 2002). In the order Carnivora, 10,000 kg of prey supports about 90 kg of a given carnivore (Carbone & Gittleman, 2002). Ectotherm carnivores have much lower food requirements than endotherms, so a given biomass of prey should support a much higher mass of carnivores, which is consistent with the subjective impression that ectotherm carnivores are far more abundant than endotherms, at least in forests. In regions with year-round warmth, the energy efficiency and body-form plasticity permitted by ectothermy may be more useful than the capacity for sustained aerobic

activity that characterises modern endotherms, particularly for ambush foragers. Endothermy has an obvious advantage only for active foragers and in the subtropics, where most ectotherms are inactive for part of the year.

If prey availability is the key factor controlling predator abundance, then we would expect co-existing carnivores to minimise competition by partitioning the prey resource, by type, size, period of carnivore activity (diurnal, crepuscular, nocturnal), and/or spatial distribution (arboreal vs. terrestrial, forest vs. open, wetland vs. dryland etc.). Although there is anecdotal support for all these from the Oriental Region, no quantitative study has investigated resource partitioning among more than 2–4 species and none has looked at the mechanisms allowing coexistence between members of different classes of carnivores. The usefulness of comparisons between diets determined by single-species studies is reduced by the rarity of quantitative studies, a lack of information on seasonal and geographical variation, and the fact that most Oriental studies have been done at sites from which one or more potential competitors have already been eliminated. Short-term studies at single sites can give a misleading impression of dietary specialisation, while pooling information from multiple sites and times can give a misleading impression of dietary breadth. Where good evidence for specialisation is available, the preferred prey is usually either frogs, medium to large snakes (including venomous species), skinks, birds, rodents or ungulates, presumably because these animals are both abundant and less efficiently captured by generalists. Efficient predation on skinks seems to require morphological adaptations (Greene, 1997), while snakes are protected from generalist predators by their potentially venomous bites, birds by flight, and ungulates by size and speed. The spatial concentration of frogs may favour specialisation, but the dominance of rodents in the diet of many species may simply reflect the fact that they are the most common potential prey in their size range. Indeed, rodents are the most common vertebrate prey of omnivorous species, such as many civets and foxes.

Most dietary data from the Region is anecdotal, so quantitative analyses of predator-prey size relationships must be treated with caution. For large mammalian carnivores (upwards from a 16-kg clouded leopard), the body mass of the largest prey commonly taken appears to be approximately equal to that of the predator itself, except that pack-hunting wolves and dholes regularly take much larger prey than predicted by individual body masses. The relationship appears to be different for smaller mammals (<15 kg), with small cats, civets and foxes subsisting largely on rodents weighing <20% of their own weight. Mongooses and some mustelids may be exceptions, with species for which there is dietary information reported to take prey around their own mass. Both diurnal and nocturnal birds of prey (<8 kg) also regularly take prey approaching their own body mass, as do some reptiles, including pythons, pitvipers and the Komodo dragon. In a wider survey, Carbone et al. (2007) found that mammalian carnivores fall into two broad categories: smaller species (< 20 kg) that feed on invertebrates and small vertebrates and larger species (> 20 kg) that specialise on large vertebrates near their own body mass, and that this transition is predicted by maximization of net energy gain. In the Oriental Region the transition from relatively small to relatively large endotherm prey appears to represent a switch between a diet dominated by rodents (and/or birds) (mostly <300 g) to one dominated by ungulates (and/or primates) (mostly >4 kg). The largest reptiles make the same transition ontogenetically, at body masses of around 10–15 kg in *Broghammerus reticulatus* (Shine et al., 1998a), *Varanus komodoensis* (Auffenberg, 1981) and *Crocodylus porosus* (Kar & Bustard, 1983).

Feeding on vertebrates that are already dead both increases the available food supply, since many vertebrates die for reasons other than predation, and lifts the prey size constraint. For energetic reasons, all obligate vertebrate scavengers are large soaring fliers (i.e. vultures) (Ruxton & Houston, 2004), although the bone-cracking dentition of hyenas allows them to exploit carcasses picked clean by these birds. Opportunistic consumption of carrion has been reported in most Oriental mammalian carnivores, many birds and a few snakes. Scavenging has probably been under-reported in snakes, but must also be limited by their need to swallow all food whole.

Most carnivores also eat at least some invertebrate prey. Carbone et al. (2007) suggest that the simple energetic constraint of relying on small food items makes an invertebrate diet impractical for mammals weighing more than about 18 kg, despite the apparent superabundance of invertebrates. The sloth bear (<150 kg) is the most striking exception, with its morphological adaptations for the efficient bulk harvest of social insects presumably side-stepping the "small food item" constraint. The less specialised sun bears (<65 kg) do not seem to maintain body condition on an invertebrate-dominated diet (Wong et al., 2004). The other specialist consumers of invertebrates among Oriental Carnivora are hemigaline civets, mustelids or mephitids (*Mydaus*), and all weigh <15 kg. Interestingly, the transition to a vertebrate-dominated diet occurs at much lower body weights (200–500 g) in both birds and snakes, with the 0.5–1.5 kg honey-buzzards being the obvious avian exception. It is hard to reconcile this with Carbone et al.'s general model, unless birds and snakes are much less efficient at harvesting invertebrates.

The other alternative to vertebrates is plant food, particularly fruits, which do not require a specialised digestive system. All the bears, the red panda, most civets and several canids and mustelids can survive, at least seasonally, on plant-dominated diets (Corlett, 1998). Among the vertebrate-eating birds, the hornbills, barbets, and corvids eat large amounts of fruit. Plant diets are relatively rare in reptiles and unknown in snakes, but there are at least two species of varanids that are frugivorous as adults. The ability to utilise plant or invertebrate foods must reduce competition with the more carnivorous species, but the morphological and physiological compromises of omnivory probably also reduce access to larger, faster or more aggressive prey. In all three classes of carnivores, the largest prey is taken by specialist hypercarnivores, which feed almost entirely on vertebrates (Table 1).

Table 1. Body weight of the largest mammalian prey that is commonly eaten by adult Oriental carnivores. Taxa with inadequate information or which largely consume invertebrate or plant diets are excluded. Note that the records for carnivorous reptiles (in bold) refer to large individuals and for birds (underlined) to the largest species in the genus.

Largest prey	Nocturnal, crepuscular or mixed	Diurnal
>100 kg	*Panthera leo*, *P. tigris*	*Cuon alpinus*
>50 kg	*Panthera pardus*, *P. uncia*	*Acinonyx jubatus*,
>10 kg	***Crocodylus porosus*, *C. palustris*, *Broghammerus reticulatus*, *Python molurus***, *Canis lupus*, *Caracal caracal*, *Hyaena hyaena*, *Neofelis nebulosa*	***Varanus komodoensis***
>1 kg	Bubo spp., *Canis aureus*, *Herpestes* spp., *Martes* spp., *Pardofelis temminckii*	Aquila spp., *Pithecophaga jefferyi*, Spizaetus spp., ***Varanus salvator***
<1 kg	Other reptiles, birds and mammals	Other reptiles, birds and mammals

Table 2. Sizes of the largest snakes, diurnal and nocturnal birds of prey, and mammalian carnivores in forests in the five major tropical forest regions. Data from sources cited in the text.

Taxon	Oriental R.	Africa	Neotropics	Madagascar	New Guinea
Snake	<8 m	<8 m	<4 m (<8 m)[1]	<2 m	<5 m
Diurnal bird of prey	2 kg (5–8 kg)[2]	3–5 kg	4–9 kg	1 kg	1.5–2.5 kg
Nocturnal bird of prey	1.5 kg	1.4 kg	0.9 kg	0.5 kg	1.1 kg
Mammal	130 kg	40 kg	90 kg	7 kg	0.7 kg

[1] The anacondas, which are found only near water.
[2] The Philippine eagle, restricted to four Philippine islands.

Coexistence despite extensive dietary overlap may be facilitated by interspecific aggression. Intra-guild aggression and predation is common in communities of mammalian carnivores and may significantly reduce the abundance and change the activity patterns of the victim species (Palomares & Caro, 1999; Thompson & Gese, 2007). Donadio & Buskirk (2006) show that attacks are most likely to occur when predator and prey differ in body mass by a factor of 2.0–5.4 and are more likely between species with high dietary overlap, suggesting that competition is the main motivation. In the Oriental Region, interspecific killing occurs throughout the carnivore community, not just among mammals. While the above-mentioned reviews suggest that other carnivores are generally not an important source of food—indeed, victims are often left uneaten—the omnivorous civets are consumed by pythons, eagles and big cats in the Region. It is also clear that this generalisation does not apply to the consumption of carnivorous snakes, for which there are specialist predators among reptiles, birds and mammals. This presumably reflects the much higher conversion efficiencies of ectotherm carnivores, which increases the food available to higher trophic levels.

***Comparisons with other tropical regions*. –** The estimates of potential sympatric carnivorous mammal richness given above (15–25 spp.) compare with estimates for the Neotropics ranging from <18 in western Amazonia (although 15 is the maximum actually recorded) and <15 in Central America (Voss & Emmons, 1996). Diversities of mammalian carnivores are lower still in African forests, which have no canids or bears and only two cats (Corlett & Primack, 2011). In contrast, Oriental raptor and snake communities are considerably less diverse than in the Neotropics (Thiollay, 1985; Greene, 1988), while African forests appear to be more similar to Asia. The estimated potential total of 45–65 vertebrate-feeding species in Oriental forests appears to be a lot lower than in the Neotropics (e.g. >100 at La Selva, Costa Rica; Greene, 1988), although it is very difficult to be sure that the numbers are truly comparable. Africa has the most diverse non-forest carnivore communities and a large component of the community of open habitats in the western Oriental Region consists of species and genera that also occur in Africa.

Small vertebrates (<1 kg) are faced with such a wide range of potential reptilian, avian and mammalian predators in the forests of the Oriental, African and Neotropical Regions that the differences in predator diversity noted above seem unlikely to have much impact on prey biology. For larger prey, however, the differences may be more significant (Table 2). The Oriental mainland lacks a diurnal raptor equivalent to the Neotropical harpy eagle (*Harpia harpyja*) or African crowned eagle (*Stephanoetus coronatus*), while African forests have no equivalent of the Oriental tiger. Even the Neotropical jaguar (*Panthera onca*), which is closely related and can kill the largest prey available, takes far more small prey (<10 kg) than any tiger (Garla et al., 2001). The green anaconda (*Eunectes murinus*) can grow heavier than any Asian or African python, but unlike pythons they are never found away from water.

Tropical islands support only a subset of the mainland carnivore fauna. In the Oriental Region, Borneo lacks both tigers and leopards, despite its large size and relatively recent overland connections with continental Asia, while raptors and/or snakes are the top carnivores in the Philippines and on Sulawesi, which have never been connected. The giant islands of Madagascar and New Guinea have never had overland connections with any region that supports Carnivora, and over-water colonisation by members of this order has occurred, respectively, once and never (Corlett & Primack, 2011). Madagascar has only a single mammalian carnivore >2 kg, the 5–12-kg, cat-like, fossa (*Cryptoprocta ferox*), which specialises on arboreal lemurs, and no really large raptors or snakes (Table 2). The largest mammalian carnivore in New Guinea is a marsupial, the 700-g New Guinea quoll (*Dasyurus albopunctatus*), and the top carnivores are birds, varanids and constricting snakes (Corlett & Primack, 2011). The extensive rainforests of Miocene northern Australia had giant marsupial carnivores, but they died out as the continent became drier, while the rainforests of New Guinea are apparently too young to have evolved substitutes.

Threats. – The cheetah is the only documented extinction of an Oriental carnivore in historical times, but many additional species are under threat from a variety of causes. Most mammalian carnivores in the Region are threatened locally, regionally or globally by hunting, largely for the huge regional trade in wild animals and their body parts (Corlett, 2007). All the larger cats and many of the smaller species are hunted for their skins, bones and other body parts. Bears are threatened by the trade in bear parts, particularly the gall bladders used in traditional Chinese medicine. The larger civets have been hunted to near regional extinction for food in China and elsewhere, and most species are exploited at least locally for food, skins or musk. Even mongooses and smaller mustelids are locally exploited for a variety of purposes. Tigers and probably other large carnivores are also threatened by depletion of prey populations. In addition, big cats, bears and canids, as well as many smaller species, are persecuted because of the real or perceived dangers they pose to people and/or their livestock. Habitat loss, degradation and fragmentation are undoubtedly also major threats to mammalian carnivores in the Region, but for most species in most of the Region the current hunting pressure maintains populations well below the potential of the surviving habitats.

Hunting appears to be a relatively less significant problem with owls and diurnal birds of prey, although many species are hunted locally for food, medicine, trophies, sport, pets or trade and the impacts have been little studied (Thiollay, 1998; BirdLife International, 2003; Naoroji, 2006). Carnivorous birds are threatened largely by habitat (particularly forest) loss and degradation (Thiollay, 1998; König et al., 1999; Ferguson-Lees & Christie, 2001; BirdLife International, 2003). Even species adapted to natural open habitats are threatened in many areas by agricultural intensification and, probably, by the massive use of pesticides (Thiollay, 1998). Reptiles in general seem to be less sensitive to habitat loss and fragmentation than birds or mammals (Brook et al., 2003). Crocodilians and turtles are exploited pantropically, but the high-volume snake trade centred on China (Zhou & Jiang, 2005) is peculiar to the Oriental Region. Snakes are used in China for food, leather and medicine, and there is a general preference for larger species, including members of the genera *Elaphe*, *Ptyas*, *Zaocys* and *Bungarus*, but the impacts of this trade on snake densities and community structure are unknown.

Conservation. – Carnivores have often been used as 'flagship species' for conservation projects in the Region. Although there is a risk that the more glamorous carnivores could divert a disproportionate share of limited conservation resources, there are also both theoretical reasons and some empirical evidence that justifies a focus on carnivores in order to achieve wider conservation goals (Sergio et al., 2006). In theory, at least, the most tractable of the problems outlined above should be hunting and trade, since enforcement of existing laws could have a big impact (Corlett, 2007, 2009). Although there are recent signs that this issue is being taken more seriously by regional governments, it is hard to be optimistic that actions will match the words. Demand reduction through education is slower, but is an essential complement to enforcement. Not all persecution of carnivores is for consumption or trade, however. Crocodiles, snakes, tigers, leopards, lions, hyenas, wolves and bears kill people and their livestock in the Region, and numerous smaller carnivores take poultry, so some form of compensation for local people will often be needed to reduce persecution. It has been suggested that direct payments to local communities that are tied to wildlife abundance are a potentially more effective conservation tool than the traditional payments for wildlife damage (Nyhus et al., 2005), but empirical evidence for this is currently lacking.

Expanding the existing protected area system and reducing the degradation and fragmentation of habitats outside this system are equally urgent, but are often in conflict with both government development policies and the perceived interests of the regional political elites. The general problems of tropical forest protection and some possible solutions are considered elsewhere (Corlett, 2009; Corlett & Primack, 2011), but the low densities and large home ranges of many vertebrate carnivores will require protected areas that are much larger than most that currently exist in the Region. On the plus side, however, is the fact that some vertebrate carnivores—but by no means all—can apparently persist in anthropogenic habitat mosaics if they are protected from direct persecution. Identifying which species are at risk and from what is a key task for the immediate future.

Carnivore introductions. – Among the known amphibian introductions to the Region, only the North American *Lithobates catesbeianus* (many sites) and the Neotropical *Bufo marinus* (in the Philippines and Ryukyu Islands) pose a potential threat to other vertebrates (Lever, 2003). No reptilian introduction from outside the Region is a threat to terrestrial vertebrates, but the many (and probably under-reported) translocations of Oriental snakes within the Region (Brown & Alcala, 1970; Lever, 2003; de Lang & Vogel, 2005) may

have had an impact, particularly on smaller islands with an impoverished native snake fauna. Moreover, the greater the ability of a non-native species to invade natural habitats, the less likely it is to be recognised as an introduction. There are no records of non-Oriental Carnivora established in the Region, although the ancestral populations of Oriental feral cats and dogs were from outside the Region. Translocations within the Region are difficult to detect, unless they occurred in historical times, and it is likely, as with the snakes, that many more island populations of carnivorous mammals are introductions than is currently recognised. *Herpestes javanicus* has been introduced to the Amami Islands and probably elsewhere, while *Viverra tangalunga* (the source of civet, used in perfumes) and *Paradoxurus hermaphroditus* are established on Sulawesi and several islands in the Moluccas (Flannery, 1995). Sulawesi already had a native civet, but the introduction of mammalian carnivores to islands that previously lacked them altogether must have had major impacts, which have not been studied.

***Reintroduction*. –** One motivation for this review was to provide the baseline information needed for the future restoration of carnivore communities. Recent reintroductions of large carnivores in North America and Europe reflect a reversal of historical attitudes, albeit one that is by no means universal even there (Enserink & Vogel, 2006). Negative attitudes towards large carnivores in the wild are still very widespread in the Region, so reintroductions of potentially dangerous species, such as tigers, leopards and bears, are politically impossible at present. Reintroductions of birds of prey, and of small and medium-sized mammalian species (up to the size of the Asiatic golden cat, caracal or *Viverra zibetha*), would meet opposition principally from farmers, and should be politically possible in large protected areas or in regions (such as Hong Kong and Singapore) where agriculture is in decline. The practicality of such reintroductions is too broad a question to be covered here, but even failures, if well documented, would provide useful experience. Rapidly declining human birth rates throughout the Region, rural-urban migration, abandonment of marginal agricultural land, improving enforcement of conservation laws, and changing attitudes to nature, all suggest the possibility of a brighter future for those carnivore species that make it through the next few decades (Corlett, 2009).

***Research needs*. –** This review highlights the difficulties of understanding carnivore ecology from a knowledge base that, in most cases, consists largely of an accumulation of anecdotes. There is an urgent need both for detailed studies of single species over their full geographic range and for studies of entire carnivore communities at representative sites. Given the on-going conservation crisis in the Region, the priorities must be threatened species and the very few areas with near-intact communities, but we also need to understand how viable populations of the more tolerant species can be helped to persist in (or be reintroduced to) human-dominated landscapes. An explosion of new (or more widely available) techniques has made it easier to move beyond anecdotes, but most of these have so far been under-utilised (e.g. radio-telemetry, camera-traps, stable isotopes, faecal DNA, and population modelling) in the Region, with most such studies carried out by well-funded extra-regional NGOs.

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