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The behaviour and ecology of the manul

Though widely distributed across the cold arid steppe and semi-desert ecosystems of Central and Western Asia, the manul is uncommon and rarely seen. The habitat in which it lives is demanding and highly seasonal; the manul exhibits morphological, physiological and behavioural adaptations that meet the challenges of temperature extremes, variable food resources and the risk of predation from other carnivores. This chapter describes the ecology of the manul, drawing from field studies and what we have learned from the captive zoo population. We end the chapter by asking how can the manul's ecology aid our understanding of its conservation biology?

Head and Body length: ♀ 49 cm, ♂ 55 cm; Tail length: ♀ and ♂ 25 cm; Weight: ♀ average 4 kg seasonally up to 5.0 kg, ♂ average 4.1 kg seasonally up to 5.3 kg.

The manul is approximately the size of a domestic cat but with shorter legs and thick fur, which accentuates its stocky appearance. On average, they weigh 4 kg, but individuals can weigh up to 5.3 kg at the end of summer when prey are more common and easier to catch. There is little sexual dimorphism, with males only slightly larger than females (100–300 g; Ross 2009, Naidenko et al. 2014).

The manul has a distinctive appearance. The head is broad and flattened with the ears set on the sides rather than the top of the head, a trait thought to be an adaptation to aid concealment when hunting in open habitats. The forehead is marked with distinctive black spots, and horizontal black and white stripes run from the eyes to the cheeks on either side of the face. Uncommon among the cats, the manul's pupils are round; in felids this characteristic is associated with diurnal hunters and/or those found in open habitats (Malmström & Kröger 2006).

The manul's coat colour varies seasonally and geographically. The species can be found with a silvery grey, rufous grey and dark grey coat, and a single individual may adopt all of these coat colours over the space of one year (Ross 2009; Fig. 1). The manul has the densest fur cover of all cat species inhabiting temporary climatic zone (Heptner & Sludskii 1992). The coat is often marked by faint black striping. In winter the pelage is longer, denser and lighter in colour than the summer coat, with a pale, frosted appearance, providing warmth and improving camouflage while there is snow cover. The manul moults in the spring, which often produces an intermediate rufous coat before the thinner and darker summer coat comes in (Ross 2009). In Iran sightings

of the manul with a rufous coat colour have occurred year-round, suggesting the red morph is specific to the region (Farhadinia et al. 2016). The manul's tail is distinctly banded, with narrow stripes ending in a dark tip. Coat colouration is supremely camouflaged on a rocky steppe background. When motionless the manul resembles a small stone, or blends onto the stone it is crouching upon. Its background matching characteristics allow it to vanish in rocky habitats (Ross 2009, Ross et al. 2012; Fig. 2). In addition, the manul's white belly and under parts improve camouflage by balancing the effects of sunlight on the top darker fur and self-shadowing on the white underside, making it particularly difficult for aerial predators to spot while it is on the move (Ruxton et al. 2004).

Origin

Although once included within the genus *Felis*, the manul is now classified as the sole species in the genus *Otocolobus*. Its classification is based on its unique morphology and its distant genetic relationship to both the *Felis* (wildcat) and *Prionailurus* (leopard cat)

lineages. Evidence suggests that *Otocolobus manul* diverged from a common leopard cat ancestor during the late Miocene approximately 5.9 million years ago. The manul is grouped within the leopard cat lineage alongside the leopard cat *Prionailurus bengalensis*, fishing cat *P. viverrinus*, flat-headed cat *P. planiceps* and rusty-spotted cat *P. rubiginosus* (O'Brien et al. 2008). Three subspecies of the manul have been described, but only two of these are said to be feasible based on geographic distribution (Kitchener et al. 2017). Although not verified by molecular analysis and not formally recognised, the subspecies are known as *Otocolobus manul manul* and *O. m. nigripictus* (Kitchener et al. 2017).

Distribution and Habitat

The manul has a wide but patchy distribution across Eurasia's high altitude montane grasslands and steppe, from western Iran to eastern Mongolia. The largest populations can be found in Mongolia, southern Siberia and China, with the distribution becoming progressively discontinuous further west. It has been recorded in mountain steppe and semi desert foothills in Kazakhstan and eastern Kyrgyzstan. Populations in the southwest of its range (the Caspian Sea region, Afghanistan, Pakistan and northern India) are diminishing, isolated and sparse. Recent records from Bhutan, Nepal and Pakistan suggest its occurrence across the Himalaya and Karakorum mountains, but despite large snow leopard survey efforts they are rarely found in this region (Chapters 3–5).

The manul's range within the continental climatic zone is characterised by aridity and large variations in annual temperature. Temperature range can reach over 100°C, as recorded in Zabaikalskii krai, Russian Dauria



Fig. 1. A female manul in montane grassland/steppe habitat of Mongolia (Photo S. Ross).

(+48°C in summer to -53°C in winter; S. Naidenko, pers. comm.). The manul's habitat preferences influence the species' distribution within its range. Typical habitat consists of montane grassland and shrub steppe (Fig. 1), with a preference for areas with rocky outcrops, ravines or other disruptive cover (Ross 2009), and within an altitude range of 450 to 5,593 m (Werhahn et al. 2018). The manul is rarely found in very open habitats such as short grassland and lowland sandy desert basins, but when prey availability is very high in open habitats it uses these habitats on a temporary basis (V. Kirilyuk, pers. comm.). It is also not found in areas where prolonged snow cover exceeds 15–20 cm, for example the manul's north-eastern range is limited by maximum snow depths of 16–17 cm in Transbaikalia (Kirilyuk & Puzanski 1999). Due to their selective use of habitats they remain patchily distributed across their range (Heptner & Sludski 1992, Ross 2009).

At the smaller scale, a major influence on the manul's habitat usage is the constant risk of predation by sympatric aerial and terrestrial carnivores (Ross 2009). Predators of the manul include large raptors, red foxes *Vulpes vulpes*, the grey wolf *Canis lupus* and domestic dogs, they are also hunted by humans (Barashkova & Smelansky 2011, Ross et al. 2012). The manul is not a fast runner and when threatened by other predators its best line of defence is hiding out of sight, relying on their excellent camouflage and taking cover in burrows (of marmots or sympatric carnivores) or in rock crevices (Fig. 2 & 3). In general, open areas without suitable cover are avoided and habitats with disruptive cover such as ravines, rocky areas, shrub-steppe and hill-slopes are highly selected (Ross 2009, Ross et al. 2010a).

As a result, the manul uses only a small fraction of habitats available within the steppe ecosystem. Their habitat selection and specialisation is the most likely explanation for their extremely low densities.

Manuls have a dependency on refuges or dens. Dens are used on a daily basis to provide important cover from predators, for feeding, mating, giving birth, raising young, and for thermoregulation during the extremely cold winters (Fig. 4). Den availability is thought to be essential for manul survival, and a critical habitat requirement for their conservation (Ross 2009, Ross et al. 2010a). In Mongolia they mostly use marmot burrows in winter and rock crevices in the summer (Ross et al. 2010a), in Southern Siberia and Kazakhstan the den sites of sympatric carnivores are more commonly used (A. Barashkova, pers. comm.), and in Iran the manul has been observed using aged *Juniperus excelsa* tree cavities as breeding dens (Dibadj et al. 2018). Despite the range of habitats used by the manul, the presence of suitable cavities appears to be a standard niche requirement.

Feeding Ecology

The manul's diet is mainly composed of small lagomorphs and rodents. Pikas are the most important prey across its range, typically comprising over 50% of the diet and highly selected over other prey species (Heptner & Sludskii 1992, Ross et al. 2010b). As pika are 2–4 times larger than other common small mammal prey, the manul's preference for them optimises hunting efficiency and energy intake. They also consume gerbils, voles, hamsters and ground squirrels; less frequently consumed prey includes small birds, young marmots, hares, hedgehogs, reptiles

and invertebrates (Kirilyuk 1999, Ross et al. 2010b). Manuls have also been recorded eating berries (Kirilyuk 1999), scavenging from carcasses (Ross et al. 2010b), and predating on a newborn argali sheep *Ovis ammon* (Reading et al. 2005).

Hunting and their activity in general mostly takes place at dawn and dusk in order to maximise the temporal overlap with prey while minimising overlap with predators, such as diurnal raptors or other competitors. Though they may switch to a more diurnal rhythm when temperatures are at their lowest (S. Naidenko, pers. comm.). As a further measure to avoid predators, the manul mainly hunts along the edges of rocky habitats and in ravines which penetrate into open grasslands and have high densities of pika, gerbils and other small mammals. Long grass and thick shrub are also used for cover when hunting and moving through flat open grasslands in the summer (Ross 2009).

Manuls hunt by three distinct techniques: 'stalking' by creeping very slowly and stealthily around cover to locate and move close to pounce on prey; 'moving and flushing', used mainly in spring and summer by walking quickly through long grass and undergrowth to flush rodents, small birds, and grasshoppers which are then pounced upon; and 'waiting in ambush' where a manul waits outside an active small mammal burrow for the prey to emerge (Fig. 5), a technique used mostly in winter to ambush pika (Ross 2009). Following a successful kill, prey is routinely taken into dens and burrows to consume in safety in Mongolia (Ross 2009), but observations of eating prey at the capture site are also common in Russia (S. Naidenko & V. Kirilyuk, pers. comm.).



Fig. 2. A male manul showing its supreme ability to blend into a rocky background in rocky habitat in Mongolia (cat in the centre; Photo S. Ross).

Movement, density and dispersal

Similar to most other cats, the manul is solitary. Males do not help raise kittens and, as a rule, they meet females only during the mating season (Ross 2009). Males' home ranges encompass 1 to 4 female territories in the typical polygynic system of solitary felids. Research in Mongolia has shown that males have highly overlapping ranges throughout the year indicating little territoriality. However, aggressive encounters between males do occur during the breeding season indicated by fighting injuries during this time (Ross et al. 2012) and suggesting that male territoriality is associated with the breeding season and mating rights. In contrast to male home ranges, spatial overlap between females was

rare in Mongolia, but appears to be related to their relatively small home ranges, low density and the spacing of their preferred mountainous/rocky outcrop habitat (Ross et al. 2012). Several cues regulate the manul's spatial behaviour, they have been observed spraying and cheek-rubbing (Mellen 1993), which provide temporal information for conspecifics. The manul also effectively communicates through vocalisations, making a strange call sounding like a honking goose. The long-distance calls and scent marking are likely used by the manul for mate attraction and to maintain spacing (Peters & Peters 2010).

Home range size is large in comparison to other species of their size. In Mongolia, females use areas between 7.4–125.2 km², averaging 23.1 km², compared to male home ranges of 21–207 km², averaging 98.8 km² (Ross et al. 2012). Research has shown that the availability and distribution of preferred rocky habitats is one of the main stimuli affecting home range size in Mongolia (Ross et al. 2012). Home ranges appear markedly smaller in Russian Dauria with male and female home ranges averaging 27.4 km² and 10.0 km², respectively (Kirilyuk & Barashkova 2011).

Density: There are no rigorous density estimates for the manul, mainly due to their low densities and cryptic behaviour resulting in difficulty in observing and surveying the species. Ross (2009) estimated density using 3-years of radio-telemetry data, surveys and observational data in what is considered prime habitat in Mongolia. At 4–8 manuls/100 km², the cats occurred at extremely low density in comparison to other carnivores found in the area. Much higher density estimates have been found in Dauria, Russia, for example Naidenko et al. (2014) captured a total of 16 manuls in an area of 16 km², equating to a density of 100/100 km². Snow tracking in Russia has also indicated that the manul can occur at very high densities (Kirilyuk & Barashkova 2011, Barashkova et al. 2017). More research is needed to understand regional differences and temporal changes in manul density, but presumably prey density and availability, and predation pressure are the most influential factors. Nevertheless, based the majority of surveys and the scarcity of sightings across the species range, evidence suggests that low density/rarity is the more common state of manul populations.

A number of factors may contribute towards the manuls' low density, including habitat specialisation, competition and prey availability. The habitats selected by the manul only cover

10–30% of mountain steppe typically occupied by the species, restricting the amount of available habitat reduces potential density of the species. Predation by other carnivores and competition for scarce prey resources may further constrain population density. For example, in the Mongolian study area carnivore density was measured using Distance Sampling. Corsac fox *Vulpes corsac* density was approximately 40–60 foxes/100 km², red fox density was 15–25 foxes/100 km² and grey wolf density was 3–20/100 km². The area also contained a high density of large raptors. These predators constrain manul density, directly through predation, and indirectly by influencing the species habitat selection (Ross 2009). Prey density may also be influential, as higher small mammal prey density should provide better nutrition and improve kitten recruitment and survival. High prey density may also reduce predation pressure, as predators focus on the more available and easily captured small mammal prey (e.g. Korpimäki & Krebs 1996). These theories need to be tested in a high density manul population, such as those found in Dauria.

Dispersal: As is normal with all solitary animals, manuls disperse from their natal home range after maturing. Data from Mongolia indicate that this happens when the kittens are approximately 4–5 months of age. Following emigration from their natal range, sub-adults make exploratory movements before settling and establishing their own home range area about 5 to 12 km from their natal home (Ross 2009).

Unusually large dispersal movements are also commonly seen in adult manuls of both

sexes (Ross 2009). The sudden abandonment of the home range and subsequent relocation to a new area mostly occurs between August and October. Individuals have been recorded migrating a straight-line distance of 18 to 52 km, and journeys often entail crossing habitats that are not normally used. For example, one adult male was observed making an exploratory, looping excursion of 170 km over 2 months, requiring swimming across a large river twice, before settling in a new area. The high incidence of home range abandonment (50% of adults, of 29 study cats) suggests that it is an integral part of their ecology (Ross 2009). Observations of large movements have also been observed in Dauriskii Reserve, Russia (S. Naidenko, pers. comm.). The motives for such moves are unclear, but most likely include a process of disturbance or prey depletion, where their home area becomes unviable, followed by emigration and subsequent colonisation of a new 'better' area. Potential home-range disturbances may include competition with other carnivores resulting in displacement, or localised prey depletion (Ross 2009).

Reproduction and demography

The manul lives in areas of the world subject to temperature extremes, thus it is unsurprising that reproduction in the wild is highly seasonal. In Mongolia, mating occurs between December and March; this is the only time of the year that females exhibit ovarian activity (Brown et al. 2002). Male sperm production also peaks during this time and dramatically drops off at other times of the year (Swanson et al. 1996). Experiments



Fig. 3. Pallas's cat showing its typical behaviour when threatened. It remains perfectly still relying on its camouflage for protection (Photo S. Ross).

in captivity using different treatments of daylight have found that the reproductive cycles of manuls are entirely controlled by day length (Brown et al. 2002).

During the mating period males pursue females to such an extent that it appears to take precedence over hunting and feeding. Extreme records have included males losing a total of 1,050 g (22%) over the course of only 14 days during the mating period, and a second male losing 800 g (19%) over 24 days (Ross 2009). Weight loss over the course of winter is also common in females, but most likely due to the scarcity of prey (Ross 2009, Naidenko et al. 2014). When females enter oestrus, males 'shadow' females for 2–3 days, protecting her from advances by other males. Mating appears to occur within marmot burrows or other crevices, presumably to protect the couple from predators (Ross 2009).

Gestation is 66–75 days and litter size averages 3–4 kittens in captivity (Swanson 1999),

but females may give birth up to 8 kittens. Kitten mortality in the wild is high with approximately 68% of kittens dying before dispersal. Surviving kittens reach independence and disperse at 4–5 months. A radiotracking study in Mongolia showed that sub-adult females may mate and reproduce at 10 months of age (Ross 2009). Their reproductive lifespan in captivity is approximately 9 years, but there is a decrease in fecundity after 6 years and very few females give birth after 8 years of age (Barclay 2013).

The lifespan of the manul in the wild may be up to 6 years, though they can survive up to 12 years in captivity. Predation is the main cause of mortality in the wild. Most predation occurs in winter, from January to April, when vegetation cover and prey density is low, increasing their exposure to predators (Ross 2009). In Mongolia large raptors accounted for 38% of known deaths, while predation by domestic dogs and hunting by people accounted for an

additional 53% of known mortalities, wolves are also a known predator, and smaller carnivores such as badger *Meles meles* and red fox occasionally kill manuls most likely on a competitive basis (Ross 2009, V. Kirilyuk, pers. comm). Mortality due to predation by domestic dogs has also been recorded in Iran, Russia and China, and appears to be a major threat to the wild population (Ross 2009, Barashkova & Smelansky 2011, Farhadinia et al. 2016). In Mongolia survival data showed that on reaching maturity at 1 year of age, adults have approximately 50% chance of surviving until 3 years (Ross 2009).

Disease

Captive manuls, particularly kittens, have a unique and marked susceptibility to infectious agents, especially *Toxoplasma gondii*. The manul is suspected to be naïve and susceptible to the agent due to lower occurrence of toxoplasma in the wild. Though 2 cases of *T. gondii* antibodies were found in manul populations in the Chita region of Russia and central Mongolia (Brown et al. 2005, Naidenko et al. 2014). Naidenko et al. (2014) also recorded antibodies to Mycoplasma, Influenza A virus and Feline leukaemia virus in a sample of 16 cats. The manul is also exposed to feline immunodeficiency virus FIV in the wild. This virus does not cause death but is related to immune depletion. Interestingly the manul harbours a unique strain of the virus most closely related to the African cheetah and leopard FIV strains (Brown et al. 2010).

The conservation biology of the manul

The manul has a very wide range across central and western Asia, and because of this the population is very unlikely to go extinct in the short term. However, of more concern is localised and regional extinction, as the manul's ecology naturally disposes them to threats (Chapter 8).

The manul is a naturally rare species, they are dependent on specific habitats and prey, and are easily killed on open ground. As the manul is a habitat specialist this is likely to result in increased vulnerability to the effects of habitat fragmentation and degradation. Its large home-ranges increase the probability that their ranges will overlap with human activities, disturbances and associated mortality, and be more difficult to cover by protected areas. For the manul, the availability of burrows, rock crevices and other cavities is necessary, as these are critical resources, used on a daily basis and essential for breeding.



Fig. 4. A rock crevice den-site with manul kittens (top) and a marmot burrow den (bottom). Dens are used on a daily basis by the manul and are essential for raising young (Photo S. Ross).