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MAMMALS

UNUSUAL FORAGING BEHAVIOUR OF TWO INTRODUCED MAMMALS FOLLOWING DEGRADATION OF THEIR ISLAND HABITAT

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INTRODUCTION

Robben Island (33°48'S, 18°22'E) (507 ha) is the largest offshore island off the coast of southern Africa (Crawford and Dyer 2000). Its proximity to Cape Town (13 km) has resulted in a long history of human activity on and around the island (Brooke and Prins 1986). The early introduction of alien species and the intensive addition of (predominately) Australian flora during World War II altered the natural environment substantially (Brooke and Prins 1986, Crawford and Dyer 2000). Stands of exotic trees and shrubs now dominate the island flora and a number of mammal, bird and reptile species have also become established (Brooke and Prins 1986, de Villiers et al. 2010, Sherley et al. 2011).

At least 10 mammal species have been introduced to the island since 1654, either accidentally or deliberately by man (Crawford and Dyer 2000). For example, European rabbits *Oryctolagus cuniculus* have been present on the island since the mid-17th century (Leibbrandt 1900) and feral cats *Felis catus* were reportedly numerous by 1881. Although cats were thought to have been extirpated by the 1950s, small numbers were encountered again in the 1980s (Crawford and Dyer 2000) and the population increased into the 2000s (de Villiers et al. 2010).



Figure 1. A European rabbit *Oryctolagus cuniculus* feeding within the canopy of a manatoka *Myoporum tenuifolium* at Robben Island, South Africa. The rabbit was between 3.2 m and 4.2 m above the ground

Between 1945 and the mid-1990s, the island was run first as a military establishment and then as a maximum-security prison. During this period, five ungulate species were introduced to the island (Brooke and Prins 1986, Crawford and Dyer 2000), including European fallow deer *Dama dama* in 1963 and bontebok *Damaliscus pygargus pygargus* in 1985. Populations of most of the introduced mammals were kept at a low level through trapping and hunting in this period, carried out predominately by staff of the then Department of Correctional Services.

Robben Island then became a museum in 1996 and a cultural World Heritage Site in 1999. Hunting and trapping were stopped during 1995 and, for all practical purposes, any control of the large mammal

populations ceased (Crawford and Dyer 2000). After 1995, the rabbit population was probably controlled by the presence of the feral cats (Aitken 1999, Crawford and Dyer 2000). An attempt to remove the cats was made during the summer of 1998/1999, when 107 individuals were killed (de Villiers et al. 2010). Examination of the stomach contents showed that European rabbit was the most frequent item in the diet (Aitken 1999). The continued presence of cats resulted in a steady decrease in breeding productivity of ground nesting birds on the island (e.g. African Black Oystercatchers *Haematopus moquini*, Braby and Underhill 2007) and a further 156 cats were removed in 2005 and 2006 (de Villiers et al. 2010) as part of conservation efforts.

As a result of the diminished top-down control over their populations, the number of herbivorous mammals present on the island increased substantially throughout the late-1990s and 2000s. For example, there were c. 12 fallow deer in 1985 and c. 44 in 1999 (Crawford and Dyer 2000), while the median counts during a series of c. 10 transect surveys in each of 2005, 2008 and 2009 were 119, 138 and 161 respectively (RBS, unpubl. data). This indicated a strong upward trend in relative abundance during the 2000s and the maximum count (307 made in 2008) suggested a density of at least 60.6 individuals km⁻². In addition, rabbits were encountered relatively rarely before the late-1990s (Crawford and Dyer 2000); fewer than 10 were seen in 1985 and there were thought to be around 100 rabbits on the island in 1999 (Crawford and Dyer 2000). However, the four-week gestation period and sexual maturation at three months of age allowed a rapid population increase after the reduction in feral cat numbers (de Villiers et al. 2010). Rabbit surveys undertaken in 2003 and 2008 suggested a 9-fold increase in rabbit abundance over five years and a maximum estimate of over 20 000 individuals in December 2008 (de Villiers et al. 2010).

This paper reports opportunistic observations of novel foraging behaviour by European fallow deer and European rabbit on Robben



Figure 2. The carcass of a European rabbit *Oryctolagus cuniculus*, hanging from a *Lycium* spp. bush on Robben Island, South Africa (left). The carcass is suspended by the right foot which had become entangled on the branch of the *Lycium* spp. bush (right).

Island during 2008. The reported behaviours are believed to have occurred in response to a reduced availability of natural browse and graze, caused at least in part by a substantial increase in herbivore density in the late 2000s (de Villiers et al. 2010).

STUDY SPECIES AND OBSERVATIONS

European rabbit

The European rabbit is thought to have been originally confined to Iberia and introduced to western Europe, north-western Africa, the Azores, the Canaries and most Mediterranean islands (Corbet 1966).

It was subsequently introduced to Australia, New Zealand and Chile, with disastrous consequences (Corbet 1966, Jaksic 1998). Rabbits were first placed on Robben Island in April 1654 (Leibbrandt 1900) and again between 1656 and 1658 (Skead 1980). By 1661, they were said to be abundant, but the occasional additional introduction may have occurred subsequently (Skead 1980, Cooper and Brooke 1982).

In mainland Europe, rabbits feed on grass and other herbaceous plants (Corbet 1966). In Chile, when herbs become scarce, they have been recorded browsing on shrubs and consuming seedlings (Simonetti and Fuentes 1983). On Robben Island, they graze and browse on a variety of plants including rooikrans *Acacia cyclops*, manatoka *Myoporum tenuifolium* and *Tetragonia* spp. They have also been observed digging up and eating the underground organs of several bulbous species (e.g. *Albuca* spp., *Trachyandra* spp. and *Oxalis cernua*; Adamson 1934, BM Dyer, pers. comm.) and encountered along the rocky shoreline of the island. Here, they were observed feeding on washed-up kelp *Ecklonia maxima* and other seaweed after March 2007 (TM Leshoro, pers. comm.).

Availability of browse probably became limiting to rabbits on Robben at least as early as April 2007, when they were seen climbing into the lower branches (less than 0.3 m above the ground) of rooikrans bushes. By March 2008 a number of observations had been made of rabbits apparently feeding on vegetation at heights ranging from 0.3–1.8 m in various locations around the island. For example, at 07:15 on 23 March 2008, a rabbit was observed at the top of a *Lycium* bush measuring c. 1.8 m in height on the north-east coast of the island and at 17:20 on 29 March 2008 another rabbit was sighted c. 1.8 m above the ground in a manatoka bush.

On 17 April 2008, at 07h25, a rabbit was spotted within the canopy of a large manatoka tree, close to the north-east coastline of the island. The rabbit was moving along a major branch at one edge of the canopy c. 3 m above the ground. At 07h27, a second rabbit was

spotted within the manatoka, c. 1.5 m above the ground. This rabbit moved quickly into the canopy and out of sight. At this point, a third rabbit was observed, c. 1 m higher than the first rabbit. The third rabbit was not standing on a major branch, but instead was sitting amongst the peripheral branches of the manatoka, c. 4 m above the ground. At 07h29, this rabbit was seen attempting to feed on the leaves of the manatoka (Figure 1). At about 07h31 another rabbit was observed trying to climb up the trunk of the tree and one rabbit was seen to exit the tree by climbing down a major branch to the split in the trunk and jumping out of the tree from a height of c. 1–1.2 m. This event was captured on video (RBS). Two rabbits remained in the tree until about 07h39 when, presumably startled by a movement from the author, both exited the tree using the above method.

Rabbits were again spotted in the same tree on two further occasions: at about 07h20 on 22 April 2008, two rabbits were observed in the same area of the tree at a height estimated at 3 m and on 24 April 2008, at 07h50, one rabbit was again observed sitting in the manatoka.

The trunk of the manatoka was near-vertical at the base and it is not clear how the rabbits entered the tree in any of the instances. The motivation for climbing the tree must have been to reach edible browse; however, when the area where the rabbits had been focused was examined on 17 April 2008, evidence of bark stripping could also be seen. The branch on which the rabbits were first observed was measured on 24 April 2008 to be at a height of 3.2 m above the ground. Based on this measure, the highest point reached by the rabbits during these observations was c. 4.2 m.

On 22 April 2008, at 07h50 a rabbit was found freshly dead, hanging from a *Lycium* bush close to a quarry at the centre of the island (Figure 2). The rabbit was suspended from a peripheral branch of the c. 1.5 m high bush. The right leg of the rabbit was entangled around the branch in a way that suggested the rabbit had got stuck whilst climbing in the



Figure 3. A male European fallow deer *Dama dama* feeding on the carcass of a European rabbit *Oryctolagus cuniculus* on Robben Island.

bush (Figure 2). The rabbit had apparently been feeding in the bush, as there was evidence of bark stripping near the carcass. When found, the rabbit was at a height of 0.7 m.

European fallow deer

It is thought that the European fallow deer was originally native to the Middle East and most of the Mediterranean region (Corbet 1966). Today, as a result of translocations by humans, they are widespread throughout Europe and present in North and South America, Africa and Australasia (Corbet 1966, Chapman and Chapman 1980, Moriarty 2004). They were brought to southern Africa from England by 1869

and three individuals were introduced to Robben Island in 1963 (Crawford and Dyer 2000).

Fallow deer are ruminant herbivores and, in Europe, have a generalist diet comprising grass, leaves and bark as well as acorns, beechmast and chestnuts depending on the season (Corbet 1966, Chapman and Chapman 1975). On Robben Island fallow deer predominately browse on rooikrans *Acacia cyclops* and manatoka *Myoporum tenuifolium* but also graze (Crawford and Dyer 2000, RBS pers. obs). From March 2007 adult males were observed breaking branches with their antlers to gain access to vegetation otherwise outside of their reach. Subsequently, during 2007 and 2008, adults of both sexes were observed eating a variety of other materials including stranded kelp, newspaper or cardboard littered on the island, and garbage rummaged from bins.

At 07h50 on 24 March 2008, an adult male fallow deer was observed feeding on the carcass of a European rabbit in the centre of a well-used road on Robben Island. On several occasions the animal was observed removing pieces of flesh from the carcass and chewing behaviour was noted. At one point, the rabbit became caught under the deer's right fore-foot and it was able to pull several pieces from the carcass over a period of c. 2 minutes. On at least three occasions, the deer lifted the body of the rabbit clear from the ground in an attempt to feed on it. For c. 10 minutes, the deer alternated between feeding directly on the animal, licking parts of the carcass and vigilance behaviour. During this time, it allowed a 10 m approach. The event was captured on video and photographed (Figure 3). At approximately 08h00 the deer was scared away from the carcass by a person passing close by. At this point, the carcass was examined and confirmed to be that of a European rabbit. It is not known how the rabbit was killed, but the position of the carcass makes vehicle strike a likely cause. From the state of the carcass *rigor mortis* had not yet

set in (Gracey et al. 1999, p. 61), so it is likely that the rabbit was killed earlier that morning.

DISCUSSION

Without appropriate control methods herbivore populations have the capacity to influence the floral structure and species composition of an ecosystem (e.g. Gill 1992, Scott and Kirkpatrick 2008). European fallow deer are known to impact upon natural forest and plantations by killing or retarding the growth of trees in Great Britain (e.g. Putman and Moore 1998) and European rabbits have been recorded killing trees in Australia through ring-barking and grazing new growth (Wimbush and Forrester 1988). Rabbits can have rapid, widespread and prolonged impacts on island ecosystems (see references in de Villiers et al. 2010). At sub-Antarctic Macquarie Island, rabbit numbers increased rapidly after the removal of feral cats (Bergstrom et al. 2009); within six years they had substantially altered floral species composition and increased the rate of erosion (Scott and Kirkpatrick 2008). In South Africa, rabbit grazing had led to poorer plant species diversity on Robben Island than in similar areas on the adjacent mainland by the 1930s (Adamson 1934) and during the 1908s, there was better vegetation cover on Meeuw Island, where rabbits were always scarce and extinct by 1977, than on Schaapen Island, where rabbits were still present (Cooper and Brooke 1982).

As most of the vegetation on Robben Island is introduced (Adamson 1934, Brooke and Prins 1986), species loss was not a major concern at the time. However, the intense grazing did dramatically alter the abundance of several species native to the West Coast Strandveld habitat, such as pipe grass *Ehrharta villosa* (Llyod and Linger 1986), and an apparent explosion in rabbit numbers up to 2008 seemed to coincide with severe degeneration of the island's vegetation (Figure 4 and 5; de Villiers et al. 2010). By March 2008 the availability of browse and graze had been substantially reduced over much of the island; a



Figure 4. Rooikrans *Acacia cyclops* bushes on Robben Island, 30 April 2008. A browse line is evident at c. 1.2 m above the ground.

browse-line was evident on the vegetation at ~1.2 m (Figure 4) and ground cover had been eradicated in places (Figure 5).

By the late summer and early winter of 2008, many of the herbivores appeared to have difficulty finding sufficient food. Both fallow deer and rabbits were seen stripping bark from the trunks and lower branches of trees on Robben Island prior to this (RBS pers. obs). The behaviour is known from in both species in Europe (e.g. Corbet 1966, Putman and Moore 1998) and generally indicates low food availability in deer (e.g. Verheyden *et al.* 2006). In February 2009 the rabbit population



Figure 5. A house at the south end of Robben Island, photographed on 23 March 2004 (top left), 11 May 2008 (bottom left) and 6 June 2016 (above). The photographs were taken after the austral summer (the dry period in the region) and before the winter rains had started. Note the absence of ground cover in the 2008 image (bottom left) and that the shrubs in the foreground and background (to the right of the house) appear to have been browsed above ground level.

on the island was estimated to have decreased to one-quarter of what it had been in November 2008, probably as a result of food limitation, with many rabbit carcasses observed across the island at that time (de Villiers et al. 2010). Moreover, there are references to rabbits climbing trees to forage in times of drought, and thus poor food availability, from Australia (e.g. Department of the Environment and Heritage 2004) and it seems likely that the rabbits foraging in the trees on Robben Island were attempting to access browse otherwise unavailable to them.

The other large herbivores also seemed to be having difficulty finding food during 2008. The number of bontebok on the island declined from at least 21 individuals in September 2007 to only two by April 2008 (RBS unpubl. data), probably because of a substantially reduced coverage of pipe grass (Adamson 1934, Lloyd and Linger 1986). Bontebok are almost exclusively grazers, with a strong preference for short grasses and new growth (Kingdon 2003, Skinner and Chimimba 2005); with little of this available, the last two died by May 2008 (de Villiers et al. 2010).

Food shortage may, thus, have explained the scavenging behaviour of the fallow deer; however, the drivers of such behaviour are not clear cut. The consumption of animal matter has been reported for several other herbivorous species (Bazely 1989) and may be directly related to nutritional stress in some cases. For example, carnivorous behaviour associated with both predation and scavenging has been recorded in the common hippopotamus *Hippopotamus amphibius* during periods of severe food shortage (Dudley 1996, 1998).

These behaviours may also be indicative of a more general and widespread ability in herbivores to learn to exploit readily available and nutritious food sources, or to gain access to specific elements otherwise lacking in their diet. In the case of white-tailed deer *Odocoileus virginianus* feeding on fish on North Manitou Island (NMI), U.S.A., the carcasses contained a greater level of crude protein and higher energy content than the natural browse or graze available (Case and McCullough 1987). In addition, many herbivorous mammals chew or ingest animal bones, termed osteophagia, likely in attempt to obtain calcium (Ca) and phosphorus (P) (Bazely 1989). Carnivory, as apparently observed here, has been suggested as an extreme form of osteophagia, but analysis on giraffes *Giraffa camelopardalis* suggested that osteophagia does not provide a substantial source of Ca and P as digestion of bones in the rumen is poor (Bredin et al. 2008). Thus, consumption of animal matter could also relate to deficiencies in other substances such as protein.

Osteophagia seems an unlikely driver for the observations described here as the deer was observed to be pulling directly at the flesh of the carcass (Figure 3). Within the suborder Ruminantia, free-ranging cattle *Bos* spp. have been recorded feeding on rabbit bones, faecal pellets and whole carcasses in Europe (WallisdeVries 1996) and cattle (Nack and Ribic 2005), white-tailed deer (Pietz and Granfors 2000), reindeer *Rangifer tarandus* (Abraham et al. 1977), domestic sheep *Ovis aries* and red deer *Cervus elaphus* (Furness 1988a,b, Pennington 1992) have all been documented eating or removing the eggs or young from bird nests in North America and Europe. Scavenging from carcasses has previously been recorded in two species of Cervidae. Reindeer have been recorded feeding on carcasses of lemmings (*Lemmus* spp.) and fish (Chernov 1985, p. 131, 176) and white-tailed deer have been recorded eating dead fish (e.g. Severinghaus 1967, Shea 1973), often in large quantities (Case and McCullough 1987). However, to my knowledge this is the first reported incidence of carnivorous behaviour in the European fallow deer.

It remains unclear exactly what led to the behaviours reported here. The scavenging behaviour could also have been driven by thirst; the deer could have been attempting to extract fluids from the carcass. However, standing water is continuously available to the large mammals within c. 500 m of where the observed behaviour took place. It seems more likely that the utilization of the carcass was instead related to nutritional stress or some need to gain specific nutritional value. Whether this was the result of specific nutritional deficiencies in the vegetation on the island or vegetation degradation though heavy grazing is unclear, though the concurrent observations of rabbits climbing trees to reach browse is suggestive of the latter.

In 2009, a control programme was initiated (de Villiers et al. 2010) and both fallow deer and rabbit numbers were substantially reduced. To my knowledge, neither behaviour described here has been observed

since, while both ground cover (Figure 5) and browse levels have recovered substantially on the island. However, fallow deer, rabbits and two other large herbivore species still occur on Robben Island; continuous management or eradication will be necessary to avoid a similar situation to the one described here arising in the future.

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