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THE DIET OF THE TASMANIAN DEVIL, *SARCOPHILUS HARRISII*, AS DETERMINED FROM ANALYSIS OF SCAT AND STOMACH CONTENTS

by David Pemberton, Sam Gales, Belinda Bauer, Rosemary Gales, Billie Lazenby and Kathryn Medlock

(with two text-figures, one plate and five tables)

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Knowledge of the diets of carnivores is an essential precursor to understanding their role as predators in ecosystems. To date, understanding of the diet of Tasmanian Devils, *Sarcophilus harrisii*, is limited and based upon largely qualitative descriptions. We examined the diets of Tasmanian Devils at six sites by identifying undigested hair, bone and feathers found in their scats. These sites range across different habitat types in coastal and inland Tasmania, and encompass devil populations that are known as both free of the Devil Facial Tumour Disease (DFTD) and populations that are infected by the disease. Tasmanian Devil scats at coastal sites (n=27) contained ten species of mammal, as well as birds, fish and insects. Scats collected from inland sites (n=17) were comprised of six mammalian species, birds and invertebrates. The most common food items were birds, Common Brushtail and Ringtail possums (*Trichosurus vulpecula* and *Pseudocheirus peregrinus* respectively), Tasmanian Pademelons (*Thylogale billardierii*) and Bennett's Wallabies (*Macropus rufogriseus*). Of all the scats, 61% contained only one food group, 32% contained two groups, 4% contained three food items and only one scat (2%) contained four food groups. We supplement this information with stomach contents from road-killed devils, and compare our results with those of previous studies, with a view to furthering our understanding of the ecology of the threatened Tasmanian Devil. Such information will be important for the management of wild and captive devil populations, particularly in light of DFTD.

Key Words: Tasmanian Devil, *Sarcophilus harrisii*, diet, Common Ringtail Possum, *Pseudocheirus peregrinus*, Tasmanian Pademelon, *Thylogale billardierii*, Bennett's Wallaby, *Macropus rufogriseus*.

INTRODUCTION

The Tasmanian Devil, *Sarcophilus harrisii* (Owen, 1838), is the largest extant carnivorous marsupial and is unique to Tasmania. The conservation status of this endemic species has recently become endangered by an infectious disease, known as Devil Facial Tumour Disease (DFTD). The disease is a cancer that kills up to 80% of individuals in affected populations. No individual has been known to survive the disease, which has spread across over 50% of the species range (Hawkins *et al.* 2006).

Management options for the Tasmanian Devil include captive breeding programs, isolating wild populations on Tasmanian offshore islands, and isolating free-ranging populations on mainland Australia or in Tasmanian reserves. Effective management of both wild and captive populations requires a comprehensive understanding of the food requirements of the species. Surprisingly, this aspect of the biology of Tasmanian Devils is poorly understood, as to date there have been few quantitative studies of their diet.

Weighing up to 13 kg, the Tasmanian Devil is significantly larger than other carnivorous marsupials. Previous studies of the diet of the Tasmanian Devil report that the species is largely carnivorous with a variety of prey species being consumed. Fleay (1952) documented anecdotal information on the diet of the species. Guiler (1970) analysed the diet of Tasmanian Devils at Cape Portland (northeast Tasmania) and Granville Harbour (western Tasmania) based on scats and stomach contents and Green (1967) examined the stomach contents of 30 Tasmanian Devils from northeast Tasmania. An assessment of the diet of the Tasmanian Devil at Cradle Mountain was reported by Jones & Barmuta (1998) although this study characterised the diet in categories of

prey body mass rather than by species composition. Taylor (1986) examined 28 Tasmanian Devil scats collected from the upper Henty River region of western Tasmania, and prior to the present study, this was the only quantitative study that reported on species identification of prey remains based on sectioning and microscopic identification of fur according to the standard technique of Brunner & Coman (1974).

By adopting a quantitative approach, the present study aims to identify the prey consumed by Tasmanian Devils at six sites. These include three coastal sites in western Tasmania (Temma, Discovery Beach and Sandy Cape), and three inland sites, (Togari, Fentonbury and Bronte) (fig. 1). These sites comprise a range of habitat types, as well as populations that are known to be either free of DFTD, or infected by the disease. Here, we describe the diets of devils at this range of sites, and conduct a meta-analysis of this and previous dietary studies of the species. Our results will not only further our understanding of the ecology of this threatened species, but also provide information important for the management of wild and captive populations.

MATERIAL AND METHODS

Diet Determination

The diet composition was determined by identifying prey remains in the scats of devils. In this study, a scat was defined as a single formed stool. Scats were collected from trapped devils at all sites except Sandy Cape where they were collected from latrines. Tasmanian Devils typically deposit faeces at regularly used latrines, and depending on population size,

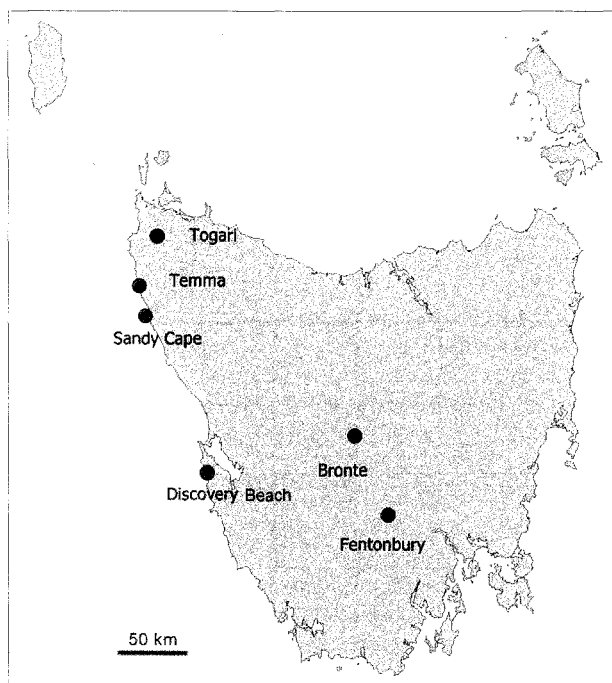


FIG. 1 — Locations where Tasmanian Devil scats were collected for analysis in this study (red indicates inland sites, and blue indicates coastal sites).

numerous devils may use one latrine. These are often near a creek crossing or other water source (Owen & Pemberton 2005). Tasmanian Devil scats can be differentiated from other carnivore scats by their larger size and shape, being tightly twisted and cylindrical (Triggs 1996). Only fresh scats were collected. The stomach contents of nine Tasmanian Devils that were accidentally killed on roads were also examined to compare the results from scat and stomach contents.

Sampling sites and times

Tasmanian Devil scats were collected from three coastal and three inland sites between October 2006 and April 2007 (fig. 1, table 1). Scats were collected as a part of the current study or were contributed to the study from collections undertaken by the Tasmanian Museum and Art Gallery (TMAG) or Department of Primary Industries and Water (DPIW).

Coastal sites

Temma is located south of the Arthur River and north of the Sandy Cape study site on the west coast of Tasmania. There is one gravel road into the area which is frequented by shack owners, fishers and recreational users. The coast is characterised by sandy bays and rocky headlands with Marram Grass, *Ammophila arenaria* L., covered dunes and coastal scrub bounding on wet marshes and tea tree scrub. Cattle are grazed seasonally on the coastal strip and tree farms (predominantly *Eucalyptus nitens* Maiden) are currently being developed in the area.

Sandy Cape is south of Temma on the edge of and included in the Tarkine National Park. The area is similar to Temma and includes areas of grazed land. The Sandy Cape area is dominated by sand dunes. The stable dunes are vegetated with coastal scrub and heathland. Common Wombat, *Vombatus ursinus* (Shaw, 1800), burrows are common in the dunes.

Discovery Beach is located south of Macquarie Harbour on the west coast. It is visited by few and supports a rich fauna including significant numbers of Tasmanian Devils. The coastal scrub is bounded by tea tree forest (*Leptospermum* spp.), eucalypt woodland (*Eucalyptus* spp. and buttongrass moorland (*Gymnoschoenus sphaerocephalus* (R.Br.) Hook.f.). The dense tea tree forests make for ideal denning habitat for devils (N. Mooney pers. comm.).

TABLE 1
Details of the location and dates of the scat collections analysed in the study

	Location	Number of scats collected	Month scats collected
<i>Coastal sites</i>			
Temma	41°13'58"S; 144°41'38"E	2	March 2007
Sandy Cape	41°25'0"S; 144°45'00"E	18	October 2006
Discovery Beach	42°23'25"S; 145°14'00"E	7	March 2006
Total coastal scats		27	
<i>Inland Sites</i>			
Togari	40°55'34"S; 144°54'24"E	8	March 2007
Bronte	42°05'24"S; 146°23'40"E	5	April 2007
Fentonbury	42°36'45"S; 146°46'00"E	4	April 2007
Total inland scats		17	
Total scats		44	

Inland sites

Togari is in the northwest of Tasmania, located 50 km west of Smithton. The habitat is dominated by wet sclerophyll forests and Blackwood, *Acacia melanoxylon* R.Br. and tea tree swamps. There is extensive logging and associated vehicle use of the area.

Bronte is located on the edge of the Central Plateau, and the habitat is dominated by eucalypt forests, buttongrass plains and grassland valleys. The area is extensively logged and grazed. There is widespread shooting of wallabies and possums in the area. DFTD is prevalent in the devil population in this area.

Fentonbury is a rural landscape comprised of dry sclerophyll forests and improved pastures. DFTD is prevalent in the devil population in this area.

Stomach analysis

Carcasses of nine Tasmanian Devils that had been accidentally killed on Tasmania's roads were provided by the TMAG for analysis. The carcasses were thawed and dissected to remove their stomachs. Using forceps and scalpels, the stomachs were cut open, contents removed then brushed with a wet 4 mm paint brush to remove all contents adhering to the stomach walls. Contents were washed in hot water over a sieve to collect all remains and then air dried and stored in individually labelled zip-lock plastic bags. Later, the remains were sorted into categories including hair, bones, skin, nails and claws and unidentified objects. Sorted remains were then documented and re-bagged.

Scat analysis

Scats from trapped Tasmanian Devils were provided by the DPIW for analysis. Scats were soaked in *Virkon*, a broad spectrum disinfectant used for effective control of viruses, bacteria and fungi, for a minimum of six hours to reduce the risk of zoonoses. Scats were then palpated with tweezers to soften them and sieved with hot water to collect diagnostic prey remains. Remains were left to air dry before being stored in labelled plastic bags. Categories for sorting included hair, bones, feathers, nails, claws, skin and unidentified objects.

Analysis of prey remains

Hairs were examined under a binocular compound light microscope and identified using the Hair ID software (Brunner & Triggs 2002), which characterises hair attributes for different species such as shape of hair in cross section, size/shape of the medulla, and colour. TMAG voucher specimens were also used to confirm identification of hair and other diagnosed remains including feathers, bones and claws.

In documenting prey remains it was assumed that the remains of a species in a scat were derived from a single individual unless there was definitive evidence for more than one individual. An occurrence is therefore defined as the presence of a prey item in a scat. In the case of birds, not all remains could be identified to species level and hence the group is treated as one prey item when describing abundance data. Where bird species were identified, they are described separately. The diet composition was assessed in two ways – composition by number of individuals, and frequency of occurrence – as each method has its own form of bias

(Hyslop 1980). Composition by number was calculated from the number of occurrences of each prey item divided by the total number of occurrences of all prey items, expressed as a percentage to give the actual proportions of prey items. Frequency of occurrence of prey items is expressed as the number of occurrences of each prey item divided by the total number of scats, expressed as a percentage.

RESULTS

A total of 44 Tasmanian Devil scats that had been collected from six different sites were analysed (table 1, fig. 1). Tasmanian Devils were found to consume mammals, birds, fish, insects and plant material (table 2). The most important prey groups were mammals and birds. Over 60% of the prey items identified were mammal, most of which (56.7%) were native species. Eight species of native mammals were identified in the diet. The three species that contributed most significantly to the diet, both in terms of prey composition and frequency of occurrence, were Common Ringtail Possums, *Pseudocheirus peregrinus* (Boddaert, 1785), followed by Pademelons, *Thylogale billardierii* (Desmarest, 1822), and Bennett's Wallaby, *Macropus rufogriseus* (Desmarest, 1817). Domestic or introduced mammal species occurred relatively infrequently (9.1%), contributing 6.0% of the prey items identified.

Birds were represented by bones and feathers and two species could be confidently identified as Little Penguins, *Eudyptula minor* (J.R. Forster, 1781) and Short-tailed Shearwaters, *Puffinus tenuirostris* (Temminck, 1835). A large species of gull was represented, but the species identification could not be distinguished between either Pacific, *Larus pacificus* Latham, 1802, or Kelp gull, *Larus dominicus*, M.H.K. Lichtenstein, 1823. The remaining bird items were all small, dark brown body feathers and probably represented one species, but could not be definitively identified. As a result of this uncertainty, birds are considered as one prey group for this study.

Invertebrates were found in two scats and fish remains in another. The invertebrates found were the remains of carnivorous beetles that are associated with rotting carcasses and maggots associated with kelp in one scat.

To compare the prey items present in scats in relation to location the data were compared between coastal (Sandy Cape, Discovery Beach and Temma) and inland (Togari, Fentonbury and Bronte) sites (tables 2, 3 and 4). The small sample size restricts the conclusions that can be made relative to diversity of the diet (Glen & Dickman 2008). The food items however, clearly represent coastal-derived material which would not be found inland. For this reason a comparison is made between the two data sets in the absence of greater sample size to support an analysis of diversity of food items. This comparison shows that Tasmanian Devils at coastal sites consumed seabirds, seals and in addition scavenged on whales (pl. 1). In comparison, scats collected from inland sites comprised mammals and birds. The principal prey species of Tasmanian Devils at coastal sites, in order of both composition and frequency of occurrence, were birds (Short-tailed Shearwaters, Little Penguins and gulls), Common Ringtail Possums and Pademelons. In comparison, the principal prey species represented in the scats of Tasmanian Devils at inland sites were Bennett's Wallaby and birds, followed by Pademelons and Common Brushtail Possums in equal representation.

TABLE 2
Food items in 44 Tasmanian Devil scats from coastal and inland sites in Tasmania

		Coastal	Inland	Total (n) ¹	Composition ² (%)	Frequency ³ (%)
Number of scats		27	17	44		
Native mammal						
<i>Ornithorynchus anatinus</i>	Platypus	2	0	2	3.0	4.5
<i>Tachyglossus aculeatus</i>	Echidna	1	1	2	3.0	4.5
<i>Vombatus ursinus</i>	Common Wombat	2	0	2	3.0	4.5
<i>Pseudocheirus peregrinus</i>	Common Ringtail Possum	8	1	9	13.4	20.4
<i>Trichosurus vulpecula</i>	Brush-tail Possum	1	3	4	6.0	9.1
<i>Thylogale billardieri</i>	Pademelon	5	3	8	11.9	18.1
<i>Macropus rufogriseus</i>	Bennett's Wallaby	0	8	8	11.9	18.1
<i>Arctocephalus</i> sp.	Fur seal	3	0	3	4.5	6.8
Total native mammal		22	16	38	56.7	86.4
Introduced/domestic mammal						
<i>Oryctolagus cuniculus</i>	Rabbit	1	0	1	1.5	2.3
<i>Bos taurus</i>	Cattle	1	1	2	3.0	4.5
<i>Rattus norvegicus</i>	Norway Rat	1	0	1	1.5	2.3
Total non native mammal		3	1	4	6.0	9.1
Bird		17	5	22	32.8	50.0
Fish		1	0	1	1.5	2.3
Insects		1	1	2	3.0	4.5
Total occurrence		44	23	67		

¹ (n) is occurrence.² Composition is the number of occurrences of a prey item divided by the total number of occurrences of all items.³ Frequency is the number of occurrences divided by the total number of scats.

TABLE 3
**Food items in 27 Tasmanian Devil scats collected from coastal sites in Tasmania:
Sandy Cape, Discovery Beach and Temma**

		Sandy Cape (n) ¹	Discovery Beach (n)	Temma (n)	n	Composition ² (%)	Frequency ³ (%)
Mammal							
<i>Ornithorynchus anatinus</i>	Platypus	0	1	1	2	4.5	7.4
<i>Tachyglossus aculeatus</i>	Echidna	0	1	0	1	2.3	3.4
<i>Vombatus ursinus</i>	Common Wombat	2	0	0	2	4.5	7.4
<i>Pseudocheirus peregrinus</i>	Common Ringtail Possum	6	2	0	8	18.2	29.6
<i>Trichosurus vulpecula</i>	Brush-tail Possum	0	0	1	1	2.3	3.4
<i>Thylogale billardieri</i>	Pademelon	5	0	0	5	11.4	18.5
<i>Arctocephalus</i> sp.	Fur Seal	2	1	0	3	6.8	11.1
<i>Rattus norvegicus</i>	Norway Rat	1	0	0	1	2.3	3.4
<i>Oryctolagus cuniculus</i>	Rabbit	1	0	0	1	2.3	3.4
<i>Bos taurus</i>	Cattle	0	0	1	1	2.3	3.4
Total mammal		17	5	3	25	56.8	92.6
Bird		10	6	1	17	38.6	63
Fish		1	0	0	1	2.3	3.7
Kelp and maggots		0	1		1	2.3	3.7
Total		28	12	4	44		

¹ (n) is occurrence.² Composition is the number of occurrences of a prey item divided by the total number of occurrences of all items.³ Frequency is the number of occurrences divided by the total number of scats.

TABLE 4
Food items in 17 Tasmanian Devil scats from inland Tasmanian sites: Togari, Fentonbury and Bronte

		Fentonbury (<i>n</i>) ¹	Togari (<i>n</i>)	Bronte (<i>n</i>)	<i>n</i>	Composition ² (%)	Frequency ³ (%)
Mammal							
<i>Tachyglossus aculeatus</i>	Echidna	0	0	1	1	4.4	5.9
<i>Pseudocheirus peregrinus</i>	Common Ringtail Possum	0	1	0	1	4.4	5.9
<i>Trichosurus vulpecula</i>	Brush-tail Possum	2	1	0	3	13.0	17.5
<i>Thylogale billardierii</i>	Pademelon	1	2	0	3	13.0	17.7
<i>Macropus rufogriseus</i>	Bennett's Wallaby	1	3	4	8	34.8	47.1
<i>Bos taurus</i>	Cattle	0	1	0	1	4.4	5.9
Total mammal		4	8	5	17	73.9	100
Bird		1	2	2	5	21.7	29.4
Invertebrate		0	1	0	1	4.4	5.9
Total		5	11	7	23		

¹ (*n*) is occurrence.

² Composition is the number of occurrences of a prey item divided by the total number of occurrences of all items.

³ Frequency is the number of occurrences divided by the total number of scats.



PLATE 1

Tasmanian Devil scavenging on a long-finned pilot whale, *Globicephala melas* Traill, 1809, near Discovery Beach on the west coast of Tasmania. Photo by Jon Marsden-Smedley.

Of all the scats, 61% contained only one prey group, 32% contained two prey groups, 4% contained three prey items and only one scat (2%) contained four prey groups (fig. 2).

All five prey taxa that were identified from the nine Tasmanian Devil stomachs were also represented in the scat analyses. In the stomachs, Common Brushtail Possum occurred most frequently ($n = 4$, 57%), followed by Bennett's Wallaby ($n = 2$, 28%), birds ($n = 2$, 28%), Pademelon ($n = 1$, 14%) and rabbits, *Oryctolagus cuniculus* (Linnaeus, 1758) ($n = 1$, 14%).

DISCUSSION

Prior to the present study, the only other investigation of Tasmanian Devil diet that used diagnostic microscopic examination of hair to report upon identification of prey species was that of Taylor (1986), who analysed the hairs collected from 28 scats from one site, the upper Henty River. More recently Jones & Barmuta (1998) used hair analysis to characterise the prey species of Tasmanian Devils from analyses of scats, but their results do not provide information on species identifications, rather prey categories: large mammal, small mammal etc. The present study therefore presents a significant advance in our understanding of the diet of Tasmanian Devils.

Whilst microscopic examination of hair is a robust technique, it is important to note that there are limitations to the analyses of diet based on identification of stomach and scat contents. These limitations include lack of information on the size or age of the prey consumed, and some prey taxa, for example earthworms, may be missed completely due to their greater digestibility (Corbett 1989). With regard to differing rates in digestibility, the present study found that prey species/groups that were observed in stomach contents were also detected in scat analyses. Further comparisons between stomach and scat contents from different regions and age classes of devils would strengthen this argument. In light of relatively small sample sizes, and the lack of biomass data for estimating original prey sizes in Tasmania, the present study did not attempt to assign importance to prey items. The small sample size is largely the result of the difficulty of attaining verified devil scats. This is currently been addressed through the collection of samples from the devil monitoring program conducted by DPIW.

Comparison with other studies

Our results support previous reports that the Tasmanian Devil consumes a wide variety of prey, and is predominantly a carnivore (table 5). This is similar to the Spotted-tailed Quoll, *Dasyurus maculatus* (Kerr, 1792) (Belcher 1995, Jarman *et al.* 2007), but different from the other Tasmanian carnivorous marsupial, the smaller Eastern Quoll, *Dasyurus viverrinus* (Shaw, 1800), whose diet includes a large proportion of insects (Blackhall 1980, Jones & Barmuta 1998).

A comparison across all the studies that report on the prey species of the Tasmanian Devil clearly shows that of the 29 food types identified, mammals are the most frequently consumed taxon (table 5). Within this group, 23 species are represented, including monotremes, marsupials, placental mammals and marine mammals (pl. 1). A compelling result reported by Guiler (1970) is that Tasmanian Devils have a wide food spectrum, and consume introduced as

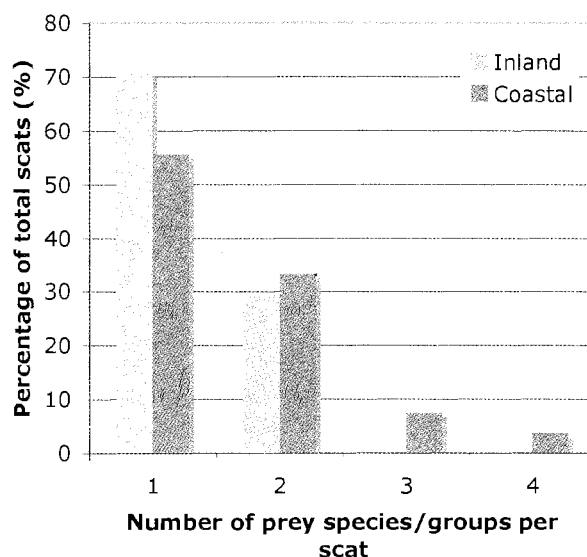


FIG. 2 — Comparison of the number of prey species/groups occurring in Tasmanian Devils scats collected at coastal and inland sites.

well as native species, but that in each area, their food was dominated by approximately three species. This result is also reflected in the comparison between studies reported here (table 5) and this also shows that the significant prey species vary between studies. Across the studies however, the most frequently reported prey species for Tasmanian Devils are Bennett's Wallaby and Common Ringtail Possums (four and five studies respectively), Pademelon (three studies) and sheep, *Ovis aries* Linnaeus, 1758, (two studies). In the present study, birds were also uniquely reported as a significant prey group. Other studies have reported that birds are of minor importance to the diet of the Tasmanian Devil (table 5). The observation that Bennett's Wallabies were one of the most commonly encountered food items in inland scats is supported by a study which found that areas with higher devil densities tend to be associated with areas where there are high spotlight counts of Bennett's Wallabies (Marvanek 2006).

Overall, the present study identified 15 food groups for the Tasmanian Devil (table 5), a diversity surpassed only by Guiler (1970) who reported a broader range of prey items (21 groups), including vegetation, insects, amphibians, Urochordata and reptiles. However, the records of Guiler (1970) included many anecdotal records and were collected over an unspecified time period. Further, whilst Guiler states whether they were made from scats or stomach contents, there is no description of how the identification was determined. The relatively high diversity reported in the present study likely results from the use of hair analysis, which provide a more robust and quantitative assessment of dietary remains than macroscopic visual assessments, as well as analysing scats that were collected from a variety of sites. Taylor (1986) also used hair analysis, but, compared to the present study, was reporting on fewer scats (28) from a single location. Jones & Barmuta (1998) also undertook hair analysis but did not provide details of species composition, so cannot be considered in this comparison, except for the major prey species that were specified.

The comparison of dietary items in coastal and inland scats in the present study showed that regional differences in diet do occur with coastal diet including food items

TABLE 5
Food items reported in the diet of the Tasmanian Devil in published accounts

		This study	Jones & Barmuta (1998)	Marshall & Cosgrove (1990)	Taylor (1986)	Guiler (1970)	Green (1967)	Fleay (1952)
Native mammal								
<i>Ornithorynchus anatinus</i>	Platypus	• ¹						
<i>Tachyglossus aculeatus</i>	Echidna	•				•		
<i>Dasyurus</i> sp.	Quoll species					•		
<i>Sarcophilus harrisii</i>	Tasmanian Devil					•	•	
<i>Antechinus</i> sp.	Antechinus species				•••			
<i>Isodon obesulus</i>	Brown Bandicoot					•		
<i>Perameles gunnii</i>	Eastern Barred Bandicoot					•		
<i>Vombatus ursinus</i>	Common Wombat	•	•••	•		•••		•••
<i>Pseudochairus peregrinus</i>	Common Ringtail Possum	••• ²		•••	•••	•••		
<i>Trichosurus vulpecula</i>	Brush-tail Possum	•				•	•	
<i>Cercartetus nanus</i>	Eastern Pygmy Possum							
<i>Thylogale billardieri</i>	Pademelon	•••		•••	•••	•		
<i>Macropus rufogriseus</i>	Bennett's wallaby	•••	•••			•••	•••	•••
<i>Rattus lutreolus</i>	Swamp Rat				•	•		
<i>Pseudomys higginsii</i>	Long-tailed Mouse				•			
<i>Arctocephalus</i> sp.	Fur seal	•						
Introduced/domestic								
<i>Ovis aries</i>	Sheep					•••	•••	
<i>Oryctolagus cuniculus</i>	Rabbit	•				•		
<i>Bos taurus</i>	Cattle	•				•		
<i>Canis lupus familiaris</i>	Dog					•		
<i>Felis catus</i>	Cat					•		
<i>Equus caballus</i>	Horse					•		
<i>Rattus rattus</i>	Black Rat	•						
Bird		•••	•		•	•	•	•
Fish		•						
Amphibian								
Reptile						•		•
Insects		•	•		•	•		•

¹ Less frequent and incidental species. ² Frequently occurring prey species.

common to the region such as seabirds, seals and whales, whereas the scats from the inland sites most commonly revealed Bennett's Wallaby and to a lesser extent birds, Pademelons and Common Brushtail Possums. These results clearly indicate and reflect differences in locations with associated differences in land use and available prey. The inland sites in the present study encompass a more rural and pastoral landscape, where in some areas there is extensive control of wallabies and Common Brushtail Possums. In comparison, the coastal locations reflect more remote and less modified environments. The Discovery Beach area is coastal heathland and wet forest, whilst the Sandy Cape site consists of coastal dunes and scrub which is grazed for only six weeks of the year. Previously Green (1967) has reported that Tasmanian Devils in some areas have benefited from the existence of the pastoral industry because of the large availability of food from this source. Studies of the diet of devils in pastoral areas (Green 1967, Guiler 1970) show that domestic stock (e.g., sheep) or native animals that have been killed on the roads or as agricultural pests (Bennett's Wallaby) have been significant food items. These results are consistent with the present study.

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The sizes of mammals whose remains were detected in scats in this and other studies ranged from mice to cattle and fur seals, with the majority coming from macropods and possums (table 5). The Tasmanian Devil therefore is not narrowly specialised in the mammals it consumes, but feeds upon both large and small species, that may be terrestrial, aquatic or arboreal. Some of the mammal species reported

Of all the scats, 61% contained only one prey group, 32% contained two prey groups, 4% contained three prey items and only one scat (2%) contained four prey groups (fig. 2).

All five prey taxa that were identified from the nine Tasmanian Devil stomachs were also represented in the scat analyses. In the stomachs, Common Brushtail Possum occurred most frequently ($n = 4$, 57%), followed by Bennett's Wallaby ($n = 2$, 28%), birds ($n = 2$, 28%), Pademelon ($n = 1$, 14%) and rabbits, *Oryctolagus cuniculus* (Linnaeus, 1758) ($n = 1$, 14%).

DISCUSSION

Prior to the present study, the only other investigation of Tasmanian Devil diet that used diagnostic microscopic examination of hair to report upon identification of prey species was that of Taylor (1986), who analysed the hairs collected from 28 scats from one site, the upper Henty River. More recently Jones & Barmuta (1998) used hair analysis to characterise the prey species of Tasmanian Devils from analyses of scats, but their results do not provide information on species identifications, rather prey categories: large mammal, small mammal etc. The present study therefore presents a significant advance in our understanding of the diet of Tasmanian Devils.

Whilst microscopic examination of hair is a robust technique, it is important to note that there are limitations to the analyses of diet based on identification of stomach and scat contents. These limitations include lack of information on the size or age of the prey consumed, and some prey taxa, for example earthworms, may be missed completely due to their greater digestibility (Corbett 1989). With regard to differing rates in digestibility, the present study found that prey species/groups that were observed in stomach contents were also detected in scat analyses. Further comparisons between stomach and scat contents from different regions and age classes of devils would strengthen this argument. In light of relatively small sample sizes, and the lack of biomass data for estimating original prey sizes in Tasmania, the present study did not attempt to assign importance to prey items. The small sample size is largely the result of the difficulty of attaining verified devil scats. This is currently been addressed through the collection of samples from the devil monitoring program conducted by DPIW.

Comparison with other studies

Our results support previous reports that the Tasmanian Devil consumes a wide variety of prey, and is predominantly a carnivore (table 5). This is similar to the Spotted-tailed Quoll, *Dasyurus maculatus* (Kerr, 1792) (Belcher 1995, Jarman *et al.* 2007), but different from the other Tasmanian carnivorous marsupial, the smaller Eastern Quoll, *Dasyurus viverrinus* (Shaw, 1800), whose diet includes a large proportion of insects (Blackhall 1980, Jones & Barmuta 1998).

A comparison across all the studies that report on the prey species of the Tasmanian Devil clearly shows that of the 29 food types identified, mammals are the most frequently consumed taxon (table 5). Within this group, 23 species are represented, including monotremes, marsupials, placental mammals and marine mammals (pl. 1). A compelling result reported by Guiler (1970) is that Tasmanian Devils have a wide food spectrum, and consume introduced as

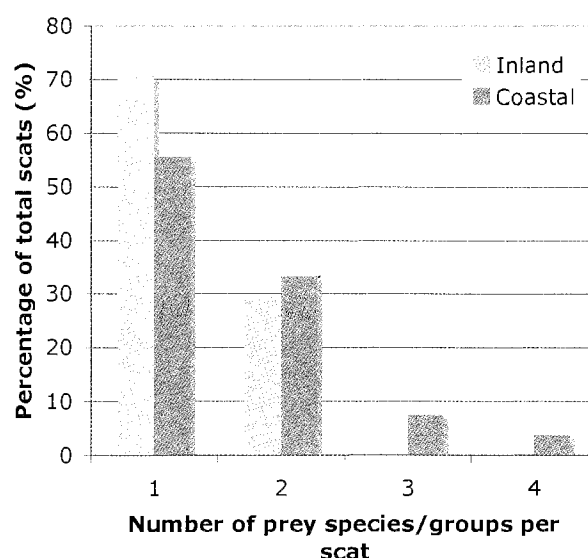


FIG. 2 — Comparison of the number of prey species/groups occurring in Tasmanian Devils scats collected at coastal and inland sites.

well as native species, but that in each area, their food was dominated by approximately three species. This result is also reflected in the comparison between studies reported here (table 5) and this also shows that the significant prey species vary between studies. Across the studies however, the most frequently reported prey species for Tasmanian Devils are Bennett's Wallaby and Common Ringtail Possums (four and five studies respectively), Pademelon (three studies) and sheep, *Ovis aries* Linnaeus, 1758, (two studies). In the present study, birds were also uniquely reported as a significant prey group. Other studies have reported that birds are of minor importance to the diet of the Tasmanian Devil (table 5). The observation that Bennett's Wallabies were one of the most commonly encountered food items in inland scats is supported by a study which found that areas with higher devil densities tend to be associated with areas where there are high spotlight counts of Bennett's Wallabies (Marvanek 2006).

Overall, the present study identified 15 food groups for the Tasmanian Devil (table 5), a diversity surpassed only by Guiler (1970) who reported a broader range of prey items (21 groups), including vegetation, insects, amphibians, Urochordata and reptiles. However, the records of Guiler (1970) included many anecdotal records and were collected over an unspecified time period. Further, whilst Guiler states whether they were made from scats or stomach contents, there is no description of how the identification was determined. The relatively high diversity reported in the present study likely results from the use of hair analysis, which provide a more robust and quantitative assessment of dietary remains than macroscopic visual assessments, as well as analysing scats that were collected from a variety of sites. Taylor (1986) also used hair analysis, but, compared to the present study, was reporting on fewer scats (28) from a single location. Jones & Barmuta (1998) also undertook hair analysis but did not provide details of species composition, so cannot be considered in this comparison, except for the major prey species that were specified.

The comparison of dietary items in coastal and inland scats in the present study showed that regional differences in diet do occur with coastal diet including food items

TABLE 5
Food items reported in the diet of the Tasmanian Devil in published accounts

		This study	Jones & Barmuta (1998)	Marshall & Cosgrove (1990)	Taylor (1986)	Guiler (1970)	Green (1967)	Fleay (1952)
Native mammal								
<i>Ornithorynchus anatinus</i>	Platypus	• ¹						
<i>Tachyglossus aculeatus</i>	Echidna	•				•		
<i>Dasyurus</i> sp.	Quoll species					•		
<i>Sarcophilus harrisii</i>	Tasmanian Devil					•	•	
<i>Antechinus</i> sp.	Antechinus species				•••			
<i>Isodon obesulus</i>	Brown Bandicoot					•		
<i>Perameles gunnii</i>	Eastern Barred Bandicoot					•		
<i>Vombatus ursinus</i>	Common Wombat	•	•••	•		•••		•••
<i>Pseudocheirus peregrinus</i>	Common Ringtail Possum	••• ²		•••	•••	•••		
<i>Trichosurus vulpecula</i>	Brush-tail Possum	•				•	•	
<i>Cercartetus nanus</i>	Eastern Pygmy Possum							
<i>Thylogale billardierii</i>	Pademelon	•••		•••	•••	•		
<i>Macropus rufogriseus</i>	Bennett's wallaby	•••	•••			•••	•••	•••
<i>Rattus lutreolus</i>	Swamp Rat				•	•		
<i>Pseudomys higginsii</i>	Long-tailed Mouse				•			
<i>Arctocephalus</i> sp.	Fur seal	•						
Introduced/domestic								
<i>Ovis aries</i>	Sheep					•••	•••	
<i>Oryctolagus cuniculus</i>	Rabbit	•				•		
<i>Bos taurus</i>	Cattle	•				•		
<i>Canis lupus familiaris</i>	Dog					•		
<i>Felis catus</i>	Cat					•		
<i>Equus caballus</i>	Horse					•		
<i>Rattus rattus</i>	Black Rat	•						
Bird		•••	•		•	•	•	•
Fish		•						
Amphibian								
Reptile						•		•
Insects		•	•		•	•		•

¹ Less frequent and incidental species.

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common to the region such as seabirds, seals and whales, whereas the scats from the inland sites most commonly revealed Bennett's Wallaby and to a lesser extent birds, Pademelons and Common Brushtail Possums. These results clearly indicate and reflect differences in locations with associated differences in land use and available prey. The inland sites in the present study encompass a more rural and pastoral landscape, where in some areas there is extensive control of wallabies and Common Brushtail Possums. In comparison, the coastal locations reflect more remote and less modified environments. The Discovery Beach area is coastal heathland and wet forest, whilst the Sandy Cape site consists of coastal dunes and scrub which is grazed for only six weeks of the year. Previously Green (1967) has reported that Tasmanian Devils in some areas have benefited from the existence of the pastoral industry because of the large availability of food from this source. Studies of the diet of devils in pastoral areas (Green 1967, Guiler 1970) show that domestic stock (e.g., sheep) or native animals that have been killed on the roads or as agricultural pests (Bennett's Wallaby) have been significant food items. These results are consistent with the present study.

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as being eaten, such as fur seals, were probably too large for the devils to have killed, their consumption likely resulting from the devils scavenging on carcasses. Scavenging on large carcasses is a behaviour common to the Tasmanian Devil (Pemberton & Renouf 1994).

Earlier studies have reported that Tasmanian Devils are inept killers that scavenge rather than hunt (Buchmann & Guiler 1977, Guiler 1970). Nonetheless, Guiler (1970) reported circumstantial evidence that devils may kill weak and debilitated lambs. The presence of fur seals in the diet in the present study suggests that the Tasmanian Devils were scavenging on beached carcasses. Dead fur seals, usually large adult males that weigh in excess of 100 kg, occasionally wash ashore on the Tasmanian coastline (Terauds *et al.* in press). A food resource such as this could last for weeks before it was too decomposed to be consumed by devils and therefore can be a rich patch of accessible food. In pastoral areas, road kills and crop protection control programs also make Bennett's Wallaby, Pademelons and Common Brushtail Possums available for scavenging by devils.

When considering the prevalence of the largely arboreal Common Ringtail Possum in the diet of the Tasmanian Devil, Taylor (1986) proposed that, rather than being an obligate scavenger, devils kill possums by climbing trees. The frequent occurrence of Common Ringtail Possums in the present study supports this suggestion that Tasmanian Devils directly hunt and actively kill this species. Young devils are capable climbers, as observed by carers of orphan devils (N. Mooney pers.comm., S. & R. Gales unpubl. data, Owen & Pemberton 2005) and also as recorded by Mrs Mary Roberts who bred devils in her zoo in the early 1900s and who remarked on their climbing ability. Roberts noted that young devils:

... frequently climb the wire-netting to the height of nearly six feet and further They were expert climbers, and although I had some specially constructed yards made, they would get up the wire-netting and walk along the top rail quite easily; at other times they would climb a pear-tree growing in their enclosure and sit in the branches like cats. (Roberts 1915: 580–581)

She also recorded an adult Tasmanian Devil climbing a high fence.

These observations led Guiler (1970) to suggest that some predation, of birds at least, may take place up trees. This climbing ability, especially as displayed by young, or smaller, Tasmanian Devils, likely explains the significant consumption of Common Ringtail Possums, which are largely arboreal.

The high proportion of birds found in the prey of devils in the present study (50% of all scats included bird remains) may be as a result of a combination of scavenging and active predation. The birds that were most often identified in the diet of the coastal devils in this study comprised both Little Penguins and Short-tailed Shearwaters. Both these species nest in burrows in coastal dunes and would be easily accessible for predation by devils. Scavenging of beach-cast birds of these species also occurs at these sites (D. Pemberton unpubl. data, N. Mooney pers. comm.). Field observations have also been made of young devils feeding on a freshly killed quail at Cape Sorell (D. Mann, B. Bauer, pers. comm.). Therefore, the unidentified brown feathers in the coastal samples may represent a species of quail, either Brown Quail, *Coturnix ypsilophora* Bosc, 1792 or Stubble Quail, *C. pectoralis* Gould, 1837. Birds were also consumed by the inland devils with 29% of scats

including bird remains. The identification of these species was not possible, but they likely include Tasmanian Native Hens, *Tribonyx mortierii* Du Bus, 1840, a large flightless water hen that flourishes on grassy paddocks.

When our results are compared and combined with those of other studies that report on the prey of Tasmanian Devils, it emerges that the feeding habits of the Tasmanian Devil include both scavenging and direct predation foraging strategies that target both mammals and birds. The prey species that are available for direct predation occur both on the ground and in trees, and vertebrate carrion is also commonly consumed.

Implications for ecological conservation and management

In the present study, the diet of Tasmanian Devils was dominated by large (Bennett's Wallaby), medium-sized (Pademelon) and small mammals (Common Ringtail Possums), as well as a significant proportion of birds. The other large mammals (wombats) that have been reported as significant prey species in the diet of Tasmanian Devils in other studies (e.g., Fleay 1952, Guiler 1970, Jones & Barmuta 1998), were largely absent in the results of the present study, occurring in less than 5% of scats.

These results have important implications for the management strategies that are being developed in response to DFTD. The clinical symptoms of DFTD, in populations that have infected individuals including Bronte and Fentonbury, are primarily detected in adults, with resistance to the disease apparently rare (Hawkins *et al.* 2006). The result of the disease, which impacts significantly on adult survival in affected populations, is that adults are rare, with most surviving individuals being young. This may well manifest in the dietary profiles of different populations.

Consequently, in populations that are affected by disease, the age of devils surviving in the population is younger than in populations that are not yet affected (e.g. the coastal sites in this study). Therefore the scats from devils at the inland sites that were dominated by Bennett's Wallaby and birds may be representing the diet of younger devils than the devils from the coastal populations on the west coast that are yet to be affected by DFTD. The prevalence of smaller prey items in the diet from inland devils as reported in this study, compared to other studies inland (Jones & Barmuta 1998), may reflect the fact that the surviving devils are now younger, and so reflect the diet preferences of younger animals (including smaller mammals and birds). Therefore, with the shifting demography of devils in affected populations, the diet will likely also change to reflect the diet preferences and foraging strategy of younger devils. Thus in more recent times, with the impact of DFTD affecting the older devils, the diet of the Tasmanian Devil may be characterised by the foraging preferences of younger animals whose prey include smaller and more arboreal species.

If the demographic age profiles in DFTD-affected populations continue to reflect mainly younger animals with few surviving adult devils, there may be implications for other mammalian predators. Jones & Barmuta (1998) report that Spotted-tailed Quolls compete for food resources (that include smaller prey) with only younger devils, as adult devils primarily depend upon large mammals. DFTD resulting in fewer surviving adult devils could therefore potentially extend the periods of competition for food resources between devils and Spotted-tailed Quolls. Balanced

against this however is the overall reduction in devil numbers as a result of population decline, thereby increasing food resources for other species, including Spotted-tailed Quolls. Therefore the net result may be an increase in the persistence of large macropod carrion and an increase in Spotted-tailed Quolls and other predators including Feral Cats, *Felis catus* Linnaeus, 1758.

Further, one of the most concerning consequences of DFTD is the enhanced potential for the establishment of Foxes, *Vulpes vulpes* (Linnaeus, 1758), in Tasmania. A commonly held view has been that the abundance of devils has prevented establishment of foxes through competition for prey and predation on denned juveniles. A reduction in devil numbers, and therefore a persistence of mammalian carrion, will provide a surplus of food, available to foxes (N. Mooney pers. comm.).

Captive management and translocation

The present study provides important information for the care of captive Tasmanian Devils. Clearly captive devils should be offered a variety of prey types, and should be held in facilities that accommodate the ability to both burrow and climb. The information from the present study will also be useful in assisting decision making when considering possible translocation sites. This study confirms that Tasmanian Devils feed on a variety of mammals and birds with a persistent consumption of Common Ringtail Possums and birds across their range. Importantly, almost 40% of scats included more than one prey item, suggesting that variety is an important element of the foraging ecology. These results suggest that choice of translocation sites must include a variety of available prey, including small mammal species such as Common Ringtail Possums. If young devils are to be caught from the wild for release in insurance sites to prevent spread of disease, then the diet and foraging strategy of the devils to be caught should be considered in light of the prey availability at the release site. The consideration of islands as translocation sites needs to accommodate these considerations. Further studies therefore need to be carried out on the seasonal and location variation in diet based on a much larger collection of scats. This is needed, particularly in response to the management actions resulting in the translocation of Tasmanian devils from and to dramatically different habitats.

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