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Scat contents of the spotted-tailed quoll *Dasyurus maculatus* in the New England gorges, north-eastern New South Wales

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Abstract. In 1313 scats of the spotted-tailed quoll *Dasyurus maculatus,* collected over 5 years from the gorge country of north-eastern New South Wales, the most frequent and abundant items were derived from mammals and a restricted set of insect orders. These quolls also ate river-associated items: waterbirds, eels, crayfish, aquatic molluscs and even frogs. Macropods contributed most of the mammal items, with possums, gliders and rodents also being common. Some food, particularly from macropods and lagomorphs, had been scavenged (as shown by fly larvae). The most frequent invertebrates were three orders of generally large insects Coleoptera, Hemiptera and Orthoptera, which were most frequent in summer and almost absent in winter scats. Monthly mean numbers of rodent and small dasyurid items per scat were inversely related to these large insects in scats. The numbers of reptile items were inversely related to the numbers of mammal (especially arboreal and small terrestrial mammal) items per scat, thus types of items interacted in their occurrences in monthly scat samples. Frequencies of most vertebrate items showed no seasonal, but much year-to-year, variation. This quoll population ate four main types of items, each requiring different skills to obtain: they hunted arboreal marsupials (possibly up trees), terrestrial small mammals and reptiles (on the ground), and seasonally available large insects (on trees or the ground), and scavenged carcases, mostly of large mammals but also birds and fishes (wherever they could find them).

Introduction

The spotted-tailed quoll *Dasyurus maculatus* is, at up to 7 kg, by far the largest member of its genus. Smaller *Dasyurus* species eat an array of live or dead animals, including rodents, birds, and reptiles, and even some fruit (Blackhall 1980; Begg 1981; Jones 1997; Soderquist and Serena 1994), but predominantly feed upon invertebrates. The present paper reports an analysis of scats of the spotted-tailed quoll, collected over 49 months in the five calendar years 1980 to 1984, from a field site in the gorge country on the eastern edge of the northern tablelands of New South Wales, where spotted-tailed quolls and their latrines are particularly numerous.

At the time the present study was undertaken, the spotted-tailed quoll had been reported (Settle 1978; Alexander 1980; Edgar 1983) as an opportunistic predator and occasional scavenger, taking mammals, birds, reptiles and arthropods. Recent studies have more fully described the species' diet (e.g. Belcher 1995; Glen and Dickman 2006*a*), and its dietary separation from sympatric carnivores in Tasmania has been fully investigated (Jones and Barmuta 1998, 2000). No previous studies have described the species' diet in gorge habitat, its stronghold in mainland temperate Australia, and few previous studies have investigated seasonal variation in scat contents over several years. Our present study aimed to determine the diet of local spotted-tailed quolls, to investigate its seasonal and year-to-year consistency, and to use our findings to comment on the species' way of life.

Materials and methods

Sampling site

The sampling site was the gorge of Salisbury Water, immediately below and for 2 km downstream from Dangar's Falls (30°40′ South, 151°45′ East). The site is 22 km south-east of Armidale, on the eastern edge of the northern tablelands of New South Wales, and is now the western tip of the Oxley Wild Rivers National Park. Salisbury Water is a small, perennial stream that, in the gorge, usually flows ~100 mm deep and 1 m wide through a boulder-strewn bed some 10 to 15 m wide; a few pools occupy the full width of the bed. In places there is a narrow band of casuarinas along the sides of the bed, with occasional fig trees. After heavy local rain, the stream may rise several metres but usually subsides within days; however, when in flood the stream may wash clean some of the quoll latrines (see below). In the collection area the gorge is ~200 m deep and its floor is 20–40 m wide. Its steep slopes carry a sparse ground cover of *Poa* and *Lomandra* tussocks, with scattered shrubs of *Acacia*, *Maytenis*, *Callitris* and *Bursaria* species. Above the gorge a narrow belt (20–300 m wide) of *Eucalyptus* woodland

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separates the gorge from adjacent tree-cleared pastures of mixed native and exotic grass species.

Non-volant mammals seen in the gorge and adjacent woodland include echidna (*Tachyglossus aculeatus*), eastern grey kangaroo (*Macropus giganteus*), common wallaroo (*M. robustus*), brush-tailed rock-wallaby (*Petrogale penicillata*), swamp wallaby (*Wallabia bicolor*), common brushtail possum (*Trichosurus vulpecula*), common ringtail possum (*Pseudocheirus peregrinus*), greater glider (*Petauroides volans*), sugar glider (*Petaurus breviceps*), feathertail glider (*Acrobates pygmaeus*), koala (*Phascolarctos cinereus*), spotted-tailed quoll (*Dasyurus maculatus*), dingo (*Canis lupus dingo*), red fox (*Vulpes vulpes*), feral cat (*Felis catus*), European rabbit (*Oryctolagus cuniculus*), and brown hare (*Lepus europaeus*). Most of these species, as well as domestic sheep *Ovis aries*, cattle *Bos taurus* and goats *Capra hircus*, occur on the surrounding pastures. No survey for small mammals has been undertaken at the site, but brown antechinus (*Antechinus stuartii*), yellow-footed antechinus (*A. flavipes*), common dunnart (*Sminthopsis murina*), house mouse (*Mus musculus*), bush rat (*Rattus fuscipes*), swamp rat (*R. lutreolus*) and black rat (*R. rattus*) have all been trapped at sites within 25 km of Dangar's Falls and may well occur there. The avifauna is typical of the NSW northern tablelands, and pools attract several waterbirds, especially black duck (*Anas superciliosa*), wood duck (*Chenonetta jubata*), white-faced heron (*Egretta novaehollandiae*), little black cormorant (*Phalacrocorax sulcirostris*), little pied cormorant (*P. melanoleucos*), dusky moorhen (*Gallinula tenebrosa*) and Eurasian coot (*Fulica atra*). The reptile, frog and invertebrate faunas of the gorge and surroundings have not been surveyed.

Scat collections

Spotted-tailed quolls at this site deposit faeces upon regularly used latrines, creating assemblages of scats on flat tops of boulders in the stream-bed (Kruuk and Jarman 1995). We found in 1980 that quolls would continue to defecate on a latrine despite the removal of scats from it. Thus by removing scats at regular intervals from the same set of latrines we ensured (in addition to their fresh appearance) that the scats were recently deposited. If collections had to be separated by more than 1 month, all scats were cleared from the latrine but only the fresher scats were collected for analysis. We identified the scats as those of spotted-tailed quolls by their characteristic smell, appearance, and place and form of deposition.

Scats were collected during 39 trips into the gorge, monthly from May 1980 to November 1981 by LRA, then less regularly up to June 1984 by SWG. Individual scats were collected separately, bagged, labelled, oven-dried and stored dry (with no signs of insect attack) until analysis began.

Scat analysis

To determine its content each scat was soaked and gently agitated in hot water to separate components, then washed through a 250-μm sieve. Items retained on the sieve were separated, grouped into type of remains (e.g. bones, fur, feathers, scales, arthropod cuticle), and stored in 70% alcohol in labelled jars. Contents of scats collected in 1980–1981 were extracted and identified by LRA, and the remainder by DJB (Boschma 1991). Between-year comparisons could have been confounded by any differences between these two operators.

We identified mammal remains mainly from hair, using characteristics of cross-sectional shape, colouring, and surface morphology (Brunner and Coman 1974). Reference samples were prepared from voucher specimens of mammals of the region. Teeth, jaw fragments, and claws aided the identification of some mammal species. We did not attempt to identify the age of individual mammals by reference to bone characteristics (cf. Jones 1997). Bird remains could sometimes be identified to order on the basis of characteristics of the downy barbules of the feathers (Day 1966). Reptiles, frogs and fishes were identified as such on the basis of scale characteristics, skin fragments and bones, with finer taxonomic resolution if possible. Arthropods could usually be identified to order on exoskeletal characteristics of limb, mouth and head parts (if present). We did not attempt to find chaetae from earthworms.

We minimised the number of individual animals represented in a scat by supposing that remains of a species in a scat were derived from one individual unless there was incontrovertible evidence for more than one. After such decisions, each individual vertebrate contributing to a scat was called an item. We made no attempt to quantify the numbers of individual invertebrates present in each scat, but counted the number of invertebrate taxa detected in the scat. We refer to the number of different invertebrate taxa present in a scat as invertebrate items, or invertebrates, per scat. This obviously underestimates the true number of invertebrate individuals in the scat.

Scat contents could then be expressed as either the kinds of items present in a scat and in collections of scats, the proportion that each food-item type formed of all identified items in the scats, the proportion of the scats in which a particular item-type was detected, or the mean number of each item-type in the average scat for each collection period. To investigate differences between years, months, seasons or recent rainfall conditions in the use of food items by quolls, we conducted one-way analyses of variance or regressions (after confirming normality of the data) on the means of numbers of each food-item type per scat in the monthly samples of scats (i.e. mean items per scat), using routines in the software package StatView (SAS Institute Inc. 1998) and accepting a probability level of $P = 0.05$ as significant (however, we also report some insignificant trends where $P < 0.10$). We defined years and months by the calendar. We collected as close to the first day of the month as possible, took the collected scats to represent the previous month's diet and recorded them under that previous month's name in the analyses. Seasons were defined as: autumn, March to May; winter, June to August; spring, September to November; and summer, December to February.

We characterised months as being wet or dry, defining a 'wet' month as one in which 10 mm or more of rain fell in at least one of the 4 weeks preceding the collection date and a 'dry' month as one with less rain than that. River flow was also classified retrospectively as 'high' (flowing fast and deep enough to impede humans), 'normal' and 'low' (when surface flow between pools was disconnected). After 3 days' heavy rainfall and flooding in May 1980, rainfall and creek-flow were low until October 1980 when moderate rainfalls occurred through to March 1982. Drought prevailed from mid-March to early

Table 1. Numbers of months in which scats of spotted-tailed quolls were sampled, the numbers of scats analysed, and the numbers of dietarily relevant items (separable items for vertebrates and indications of presence for invertebrates) found in them, in the four seasons of the study

	Season				Year					
	Summer (Dec–Feb)	Autumn (Mar–May)	Winter (Jun–Aug)	Spring (Sep–Nov)	1980	1981	1982	1983	1984	Total
Months	9	10	12	8	8	11	8	9	3	39
Scats	293	379	349	292	406	489	247	127	44	1313
Items	558	670	540	521	611	803	503	286	86	2289

September 1982, breaking in the spring of 1982. The next 2 years, the remainder of the sampling months, were close to normal in their rainfall, except for a dry spell from mid-April to mid-June 1984, and summer 1983–84, which was particularly wet.

We did not translate presence or frequency of items in scats to a measure of contribution of items to the quolls' diet (as has been done for quolls and other carnivores by, for example, Kruuk and Parish 1981, Jones and Barmuta 1998, and Jones 2003).

Results

Sampling

We collected a run of 19 consecutive monthly samples from May 1980 until November 1981, then sampled the same set of latrines 20 times in the 30 months from January 1982 until June 1984. Overall, the 39 monthly collections averaged 33.7 scats per collection and totalled 1313 scats. In the 14 months of normal or low river flow between May 1980 and November 1981, scats accumulated on the set of sampled latrines at a mean rate of 1.83 ± 0.51 (s.d.) (range 1.35–3.40) scats per day. Sampling yield was reduced when high river flow covered (or had washed scats from) some latrines.

Table 1 shows the numbers of monthly samples, scats and separable items for the five sampled calendar years and four seasons. Collections were fairly evenly distributed between seasons, but not between years.

Items identified in the scats

Complete sample

Each individual scat usually contained a variety of materials. Some were unlikely to be food remains, including soil, occasional plant material and, in three scats, picnic food wrappings (plastic and metal foil). Items of animal origin identified in scats but unlikely to be relevant to quoll diet included human hair (once), a thrip (once), a flea (once) and hairs from spotted-tailed quolls themselves (13 times, never abundantly). The last two items were probably ingested by quolls while grooming, but no specific effort was made to find all quoll grooming hairs. The samples also included remains of two adults and 145 larvae of blowflies ('gentles', of the Families Calliphoridae or Sarcophagidae) and 42 ants, which we considered were probably ingested when quolls scavenged on carcases on which those insects were feeding (see below). We omitted all these from dietary analyses, leaving a total of 2289 dietary items.

The mean number of identified items per scat in monthly collections averaged 1.87 ± 0.43 (s.d.) and did not vary significantly between months or seasons (Table 2). However, the mean monthly values in 1980 (1.51 ± 0.21) and 1981 (1.62 ± 0.19) were lower than in 1982 (2.08 ± 0.45) and 1983 (2.26 ± 0.36) ($F_{4,34}$ = 9.091, P < 0.001).

Dietary items in the scats were mostly from vertebrates (72.7%; Table 3). Mammals constituted almost four times as many separable occurrences in scats as any other class, being

Table 2. Numbers of items per scat (mean and s. d.) by seasons and for the whole year, for all items, major categories of items, mammal groups, and large insects (Coleoptera, Orthoptera and Hemiptera)

Taxon	Spring		Summer		Autumn		Winter		All year	
	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
Invertebrates	0.444	0.256	0.754	0.268	0.586	0.264	0.322	0.152	0.514	0.279
Fishes	0.120	0.169	0.130	0.174	0.251	0.250	0.119	0.167	0.155	0.194
Frogs	0	0	0.004	0.011	0.012	0.037	0.028	0.062	0.012	0.040
Reptiles	0.210	0.088	0.173	0.195	0.126	0.165	0.057	0.068	0.133	0.144
Birds	0.225	0.104	0.168	0.221	0.200	0.186	0.099	0.126	0.167	0.166
Mammals	0.844	0.251	0.818	0.372	0.842	0.363	1.013	0.120	0.890	0.288
Macropodoidea	0.417	0.260	0.339	0.177	0.291	0.109	0.403	0.127	0.362	0.171
Phalangeroidea	0.107	0.083	0.155	0.096	0.209	0.142	0.210	0.112	0.176	0.116
Dasyurids	0.026	0.045	0.060	0.088	0.040	0.058	0.049	0.052	0.044	0.061
Rodents	0.151	0.225	0.146	0.156	0.131	0.160	0.208	0.194	0.162	0.180
Other mammals	0.143	0.130	0.118	0.064	0.171	0.185	0.155	0.091	0.148	0.122
Large insects	0.135	0.179	0.416	0.292	0.279	0.230	0.099	0.121	0.226	0.238
All items	1.831	0.486	2.058	0.371	2.000	0.492	1.648	0.286	1.871	0.427

followed by insects, reptiles, fishes and birds. Frogs, arachnids, chilopods, crustaceans and molluscs were minor contributors to the total (Table 3).

Among the mammalian items (Table 4), monotremes were represented by echidna (*Tachyglossus aculeatus*) 13 times (1.3% of mammalian items). Items from metatherians (marsupials) formed 68.4% of identified mammalian items, while items from eutherians formed 19.0%. Apart from one item each from red fox (hair) and an unknown bat, the eutherian items (Table 4) were from rodents (155 items), the two exotic lagomorphs European rabbit (*Oryctolagus cuniculus*) and brown hare (*Lepus europaeus*) (25 items between them), cattle (*Bos taurus*) (eight items), sheep (*Ovis aries*) (three items), and goat (*Capra hircus*) (one item). Among the rodent items, one was identified as *Melomys cervinipes*, 24 were *Mus musculus*, and 123 were derived from *Rattus* species, among which *R.fuscipes* and *R.lutreolus* were tentatively identified.

The metatherian items (Table 4) were dominated by the superfamilies Macropodoidea (64.1% of metatherian items) and Phalangeroidea (28.1%), with Dasyuroidea contributing relatively few items (7.7%). The macropod items that could be identified to genus were from brush-tailed rock-wallaby (*Petrogale penicillata*) (48.4%), swamp wallaby (*Wallabia bicolor*) (37.4%), and *Macropus* species (*M.giganteus* and *M.robustus*; 14.3%). The phalangeroid items identified to genus were from *Trichosurus* (69.3%), *Pseudocheirus* (15.3%), *Petaurus* (13.2%), *Petauroides* (1.6%) and *Acrobates* (0.5%). Of the dasyuroid items (apart from *Dasyurus maculatus* itself, which was discounted as a dietary item because it was never represented by more than a few hairs), *Antechinus* was the most frequently identified genus. Macropods, phalangeroids and rodents led the rankings of frequencies of occurrence of mammalian orders (of eutherians) or superfamilies (of metatherians) and genera (Table 5).

Of the 168 bird items, 42 could not be further identified; the 126 that could be assigned to an order or family were evenly divided between waterbirds (38 Anseriformes, 25 Ralliformes, 3 Pelecaniformes, 2 Ciconiiformes) and land birds (51 Passeriformes, 4 Falconiformes, 2 Psittaciformes, 1 Columbiformes). Of the 241 reptile items, 18 could not be identified further, and the rest were squamates (200 from lizards, and 23 from snakes) with no remains of freshwater turtles identified in scats. Frog remains were identified in scats only eight times. Fish remains were recognised 225 times, of which eels (*Anguilla* sp.) provided 151. However, all those eel records occurred in just 7 months between February and November 1981 (132 in 5 consecutive months), when large numbers of dead eels accumulated in pools.

Of the 624 invertebrate items relevant to the quoll diet (Table 6), 33 were molluscs (both gastropods and bivalves), 9 were crustaceans (yabbies, probably *Cherax destructor*) and the rest (93.4%) were arthropods. Of the arthropod items, 301 could not be identified further, two were arachnids (spiders), and 34 were chilopods (centipedes or millipedes). The

Table 3. Broad taxonomic groupings of the 2289 separable dietary items in the whole sample of 1313 analysed scats

Note that invertebrates are recorded as only one instance (an indication of presence) of each type per scat, so the number of invertebrate items may be greatly underestimated

Taxon	No.	%
Vertebrates	1665	72.7
Mammals	1023	44.7
Birds	168	7.3
Reptiles	241	10.5
Frogs	8	0.3
Fishes	225	9.8
Invertebrates	624	27.3
Insecta	260	11.4
Arachnida	2	0.1
Chilopoda	34	1.5
Crustacea	9	0.4
Unidentified arthropods	286	12.5
Mollusca	33	1.4

Table 4. Representation of mammalian taxa or groups, by absolute and relative frequencies of items, in the whole sample of spotted-tailed quoll scats analysed in the study

No. = absolute number of items of that taxon in the whole sample; % = percentage that items of that taxon form of all 1023 mammalian items

Taxon	No.	%
Prototheria	13	1.3
Tachyglossus aculeatus	13	1.3
Metatheria	700	68.4
Macropodoidea	449	43.9
Petrogale penicillata	176	17.2
Wallabia bicolor	136	13.3
Macropus spp.	52	5.1
Unidentified macropod	85	8.3
Phalangeroidea	197	19.3
Trichosurus spp.	131	12.8
Pseudocheirus peregrinus	29	2.8
Petaurus spp.	25	2.4
Petauroides volans	3	0.3
Acrobates pygmaeus	1	0.1
Unidentified phalangeroid	8	0.8
Dasyuroidea	54	5.3
Antechinus spp.	19	1.9
Sminthopsis murina	3	0.3
Unidentified dasyurid	32	3.1
Eutheria	194	19.0
Rodentia	155	15.2
Rattus spp.	123	12.0
Mus musculus	24	2.3
Melomys cervinipes	1	0.1
Unidentified rodent	7	0.7
Lagomorpha	25	2.4
Lepus europaeus	11	1.1
Oryctolagus cuniculus	13	1.3
Hare/rabbit	1	0.1
Carnivora	1	0.1
Vulpes vulpes	1	0.1
Chiroptera	1	0.1
Artiodactyla	12	1.2
Bos taurus	8	0.8
Ovis aries	3	0.3
Capra hircus	1	0.1
Unidentified mammal	116	11.3

great majority (260, 92.2%) of the 282 identified arthropod items were insects (Table 6). Coleoptera, Hemiptera and Orthoptera contributed 91.5% of the relevant insect items. Thus most identified invertebrate items (beetles, cicadas, grasshoppers or crickets, centipedes and millipedes, mussels, snails and yabbies) were individually quite large. Of the 162 coleopteran items, 95.1% were adult beetles.

Variation between years

Monthly collections, sampled numbers of scats, and numbers of separable items differed between years (Table 1), with 1984 being particularly poorly represented. The five sampling years differed significantly in the mean number of items per scat derived from mammals ($F_{4,34}$ = 7.944, P < 0.0001), birds ($F_{4,34}$ = 4.443, P = 0.0054), and reptiles ($F_{4,34}$ = 12.205, P < 0.0001) but not frogs, fishes or invertebrates (P = 0.0962, P = 0.1074 and P = 0.0674 respectively). Analysed scats contained, on average, more mammal items per scat in 1982–1984 than in 1980 or 1981, more bird items per scat in 1984 than in 1980–1983, and more reptile items per scat in 1980–1981 than 1982–1984.

When the major groups of mammals in quoll scats were analysed separately, the numbers of items per scat differed significantly (or nearly significantly) among years for: possums and gliders ($F_{4,34}$ = 2.827, P = 0.0398), which provided more items per scat in 1982 than 1980 or 1981; small dasyurids ($F_{4,34}$ = 2.624, P = 0.0511), which provided more items per scat in 1983 than 1981, 1982 or 1984; rodents ($F_{4,34}$ = 7.732, P = 0.0002), which provided more items per scat in 1984 than all other years, and in 1982 and 1983 than 1980 and 1981; and other mammals (mainly lagomorphs and bovids) ($F_{4,34}$ = 4.125, P = 0.0079), which provided more items per scat in 1980, 1982 and 1983 than 1981, and in 1983 than in 1984.

Numbers of items per scat contributed by macropods, the commonest dietary items, did not vary between years. The overall increase in mammal items per scat in 1982–1984 came from increases not in the primary source of food (macropods), but in secondary and different groups of mammals in different years. Possums and gliders contributed particularly in 1982, dasyurids in 1983, rodents in 1982 and 1983 but particularly in 1984, and introduced lagomorphs and bovids in 1983 particularly, but also 1982 and 1984.

Variation between months and seasons

Vertebrate items per scat showed inconsistent variation between months (Fig. 1) and no vertebrate taxon (class, order or superfamily) varied significantly between months or seasons in the number of items it contributed to the average quoll scat. There was a trend towards seasonality in reptile items per scat with a significant difference between winter and spring, and significant differences in non-passerine bird items per scat between spring and winter and spring and summer (Table 7). Mammal groups showed little variation between seasons in the numbers of items they contributed to scats; however, arboreal items tended (Table 7) towards seasonality, with numbers in spring tending to be lower than those in autumn and winter (P < 0.0659 and P < 0.0559, respectively). However, invertebrates contributed fewer occurrences to scats in colder months (especially June, July and September) than in other months ($F_{11,27}$ = 2.995, P = 0.0099), so their contribution to scats varied significantly with season (Table 7). Contributions by invertebrates were greater in summer (the season of greatest contribution) than in winter and spring, and greater in autumn than winter (the season of lowest contribution) (Fig. 1). These differences were driven by the most common insect orders in the scats, Coleoptera and Orthoptera, whose occurrence in scats showed significant seasonal variation (Table 7). Beetles contri-

Table 5. Ranking, by absolute and relative frequencies of mammalian taxa, among the mammalian items in the whole sample

In total, 907 items were identified to order or superfamily and 760 to genus or species. Also shown is the number of months in which a taxon was identified in the analysed scats, out of 39 sampled months

Rank	Taxon	Items	%	Months
Order or superfamily				
1	Macropodoidea	449	49.5	39
2	Phalangeroidea	197	21.7	37
3	Rodentia	155	17.1	35
4	Dasyuroidea	54	6.0	22
5	Lagomorpha	25	2.8	18
6	Monotremata	13	1.4	7
7	Artiodactyla	12	1.3	8
Genus				
1	*Petrogale*	176	23.2	30
2	*Wallabia*	136	17.9	32
3	*Trichosurus*	131	17.2	32
4	*Rattus*	123	16.2	33
5	*Macropus*	52	6.8	15
6	*Pseudocheirus*	29	3.8	16
7	*Petaurus*	25	3.3	12
8	*Antechinus*	19	2.5	10
9	*Oryctolagus*	13	1.7	10
10	*Tachyglossus*	13	1.7	7
11	*Lepus*	12	1.6	9

Table 6. Orders of invertebrates identified in the whole sample of spotted-tailed quoll scats analysed in this study, expressed as absolute numbers of items, the proportion of all dietarily relevant invertebrate items identified to order (total = 338), and the number of months in which the order was represented (out of 39 sampled months)

Taxon	Items	%	Months
Insecta			
Coleoptera adults	154	45.6	31
Coleoptera larvae	8	2.4	2
Hemiptera	43	12.7	17
Orthoptera	33	9.8	19
Diptera adults	2		2
Diptera larvae	145		28
Hymenoptera, excluding ants	11	3.3	10
Hymenoptera (ants)	42		20
Odonata	8	2.4	4
Lepidopteran larvae	3	0.9	2
Thysanoptera	1		1
Siphonaptera	1		1
Arachnida	2	0.6	2
Chilopoda	34	10.1	13
Unidentified arthropods	301		36
Mollusca	33	9.8	10
Crustacea	9	2.7	7

buted significantly more occurrences in summer, and grasshoppers and crickets in summer and autumn, than in the other seasons.

Rainfall (as wet or dry months) had no significant effect upon the composition of the month's scats, despite an overall trend towards more large insects in wet than dry months (Fisher's PLSD mean difference = 0.202, critical difference 0.214, P = 0.0626). However, rainfall had a slight additional effect upon the seasonality of occurrence of some items in scats. For example, more large insects tended to occur in scats in wet spring and autumn collections than in dry collections for those seasons ($F_{1,16}$ = 4.128, P = 0.0591), although rainfall had no within-season effect upon large insect occurrences in summer and winter collections. We found more rodents in scat collections from dry months than wet months in autumn and winter ($F_{1,20}$ = 8.458, P = 0.0087), but not in spring and summer.

Relationships between item types

Our large number of monthly samples gave us the opportunity to investigate whether types of dietary items influenced the consumption of other types by spotted-tailed quolls. The occurrences of the major item classes in the 39 monthly collections of scats were independent of each other, with the exception of mammals and reptiles, and large insects and reptiles. Monthly mean numbers of reptile items per scat were negatively related to mammal items per scat, and separately to large-insect (Coleoptera, Hemiptera and Orthoptera combined) items per scat: reptile items per scat = 0.458 – 0.365 × mammal items per scat, R^2 = 0.537 (P < 0.0001) and reptile items per scat = 0.182 – 0.219 × large-insect items per scat, R^2 = 0.131 (P < 0.0233).

Considering the influence upon reptile items per scat of each mammal group separately, the occurrences in scats of items from arboreal mammals explained 21%, rodents 17%, small terrestrial mammals (rodents and dasyurids combined) 20%, and other mammals (i.e. non-rodent eutherians) 13% of the variance in monthly values of reptile items per scat, with all relationships being negative. Partial correlation analysis of items per scat derived from reptiles and from each group of mammals showed a highly significant negative relationship between reptile-item per scat and arboreal mammal-item per scat, holding all other variables constant (P = 0.0002). A model containing arboreal, rodent, other-mammal and large-insect items per scat as independent variables explained 39% of variance in monthly values for reptile items per scat (ANOVA $F_{3,35}$ = 9.049, P < 0.0001; regression coefficients: arboreal items per scat –0.453, P = 0.0081; rodent items per scat –0.311, P = 0.0042; large-insect items per scat –0.181, P = 0.0265).

Mean monthly bird items per scat tended to be positively related to large-insect items per scat (bird items per scat = 0.120 + 0.208 × large-insect items per scat; R^2 = 0.089, P = 0.0645) and even less confidently to mammal items per scat (bird items per scat = 0.035 + 0.148 × mammal items per scat; R^2 = 0.066, P = 0.1146). Rodent items per scat considered alone were significantly and positively related to bird items per scat (bird items per scat = 0.107 + 0.367 × rodent items per scat; R^2 = 0.159, P = 0.0118). Analysing by stepwise regression the influence, upon bird items per scat, of large-insect, reptile, macropod, arboreal, dasyurid, rodent and other-mammal items per scat, only rodent and large-insect items per scat were selected, producing a significant model (adjusted R^2 = 0.216; ANOVA $F_{2,36}$ = 6.237, P = 0.0047; regression coefficients: rodent items per scat 0.377, P = 0.0071; large-insect items per scat 0.218, P = 0.0359). Non-passerine bird items per scat showed no relationship to items from other taxa (including

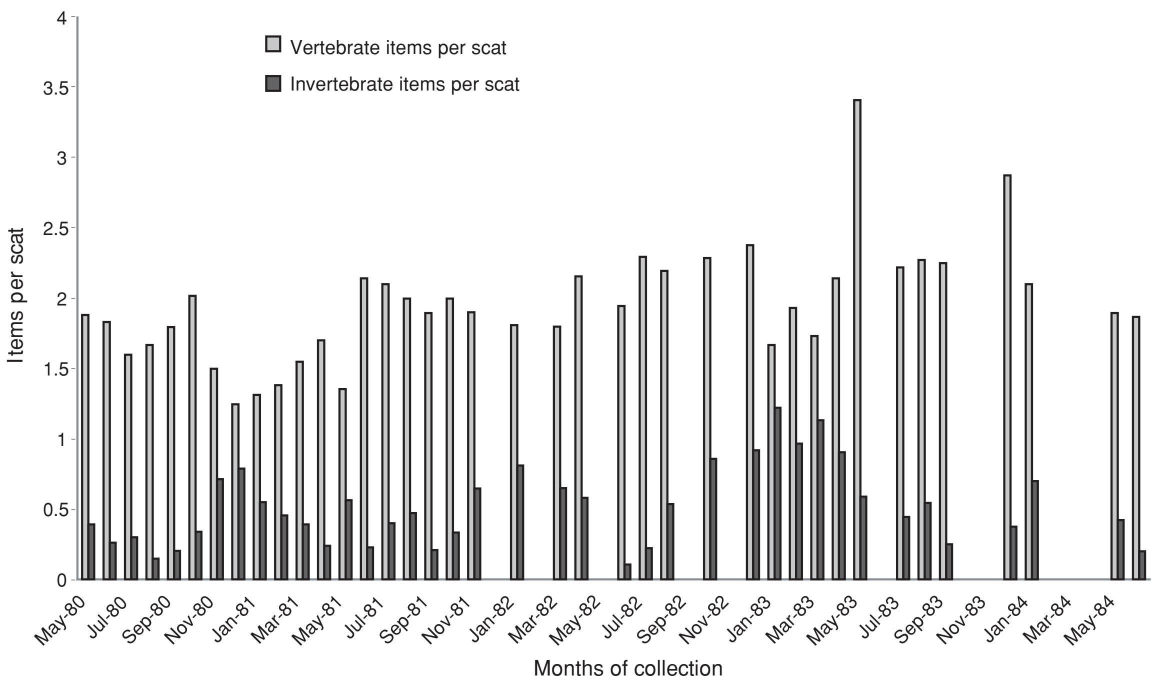

Fig. 1. Mean numbers of vertebrate and invertebrate items per scat for each of 39 monthly collections of spotted-tail quoll scats between May 1980 and June 1984.

passerine items). However, passerine items per scat were positively and significantly related to dasyurid items per scat (passerine items per scat = 0.025 + 0.802 × dasyurid items per scat, $F_{1,37}$ = 11.919, P = 0.0014) and other-mammal items per scat (passerine items per scat = 0.047 + 0.324 × other-mammal items per scat, $F_{1,37}$ = 5.426, P = 0.0254), and showed a trend towards a positive relationship with rodent items per scat (passerine items per scat = 0.035 + 0.157 × rodent items per scat, $F_{1,37}$ = 3.314, P = 0.0768).

Relationships between item types in the monthly scat samples may have varied between years. Although no relationship was found across all years between occurrences of large-insect items and items from major groups of mammals, in the monthly samples from 1982 to 1984 (years when mammal items were most frequent) occurrence of large insects in scats was significantly and negatively related to occurrence of small terrestrial mammals (rodents and small dasyurids combined): large-insect items per scat = 0.584 – 0.710 × small terrestrial mammal items per scat, R^2 = 0.425, P = 0.0018). This relationship indicates that quoll scats, in these years, contained large insects at their highest rates when they contained small terrestrial mammals at their lowest rates, and vice versa.

Presence of eels

The occurrence of large numbers of dying and dead eels in pools in the gorge in 1981 allowed us to consider the effect of the presence of one temporarily abundant food source upon the occurrence of other items in scats. We compared composition of scats during the months when eels were available and eaten with composition during other months between December 1980 and November 1981, and found no relationship between the numbers of items in the scats from eels and from birds, reptiles (considered alone) or large insects, but a weak trend (P = 0.1047) towards a negative relationship between eel items and mammal items (but still explaining 24% of the variance in eel items per scat). That relationship could not be attributed to any single group of mammals. However, multiple regression analysis showed that reptile items per scat enhanced the relationship between eel and mammal items per scat. We found a significant negative relationship between eel items per scat and the sum of mammal and reptile items per scat (eel items per scat = 1.237 – 1.145 × (mammal + reptile) items per scat, R^2 = 0.655; ANOVA, $F_{1,10}$ = 18.971, P = 0.0014). This suggests that eels, while abundantly available to be scavenged, displaced mammal and reptile items, usually the most abundant vertebrate items in the scats (in 1980–1).

Evidence for scavenging

The remains of fly maggots (of the families Calliphoridae or Sarcophagidae) in 145 (11.0%) of the 1313 analysed scats confirmed that quolls had scavenged some of their food from carcases. The maggots appeared to have passed through the gut of the quoll rather than having developed from eggs laid on the scats; no live maggots were found in fresh scats (cf. Belcher 1995). The monthly proportion of scats containing maggots fluctuated between 0 and 38%, with a trend towards fewer (5.2% of) scats containing maggots in the colder months of May–August, compared with 14.5% of scats from all other months ($F_{1,10}$ = 4.567, P = 0.0583). Median values of monthly proportions of scats containing maggots differed significantly (Mann–Whitney U-test for unmatched samples, U = 18; P < 0.05) between the samples from May to August and other months, suggesting either more fly activity or more scavenging or both in the warmer months.

We investigated whether scavenging was associated with particular food types. Presence of maggots in individual scats collected in 1980–1981 varied with the types of mammalian food items present. Maggots were present in significantly more of the scats containing items from macropods (19.9% of 311 scats) and lagomorphs (27.3% of 11 scats) than in scats containing items from arboreal mammals (7.3% of 96 scats), rodents (10.4% of 48 scats) or dasyurids (3.7% of 27 scats) (significance judged by values of Yate's corrected χ^2). Four of the 10 scats containing echidna remains also contained fly larvae, and were thus suggestive of scavenging. Using the 19 monthly collections from 1980–1981, regression analyses showed that monthly occurrences of maggots per scat bore no relationship to occurrences of all mammals combined, but showed a trend for maggots per scat to be positively associated with macropod items per scat (maggots per scat = 0.057 + 0.212 × macropod items per scat, R^2 = 0.165, P = 0.0849), while negative relationships between maggots per scat and arboreal items per scat (maggots per scat = 0.197 – 0.456 × arboreal items per scat, R^2 = 0.220, P = 0.0428), dasyurid items per scat (maggots per scat = 0.174 – 1.336 × dasyurid items per scat, R^2 = 0.226, P = 0.0399), rodents per scat (maggots per scat = 0.182 – 0.673 × rodent items per scat, R^2 = 0.135, P = 0.1212) and 'terrestrial small mammals' (dasyurids and rodents combined) (maggots per scat = 0.232 – 1.049 × terrestrial small mammal items per scat, R^2 = 0.388, P = 0.0044) were evident. The monthly rate of occurrence of maggots in scats was well predicted by a stepwise

Table 7. Analyses of variance for named items per spotted-tailed quoll scat, by season

F and P values are given. Pairs of seasons whose mean values for items per scat differed significantly (tested by Fisher's PLSD) are shown; pairs in brackets showed a trend (P < 0.07) towards difference. Seasons: Sp = spring, Su = summer, A = autumn, W = winter

Taxon	$F_{3,35}$	P	Significantly different pairs of seasons
Mammal	1.082	0.3694	Nil
Bird	1.156	0.3405	Nil
Reptile	2.342	0.0900	W/Sp
Frog	1.013	0.3986	Nil
Fish	1.089	0.3667	Nil
Invertebrate	6.410	0.0014	Su/W, Su/Sp, A/W
Macropod	1.150	0.3425	Nil
Arboreal mammal	2.498	0.0779	(A/Sp, W/Sp)
Dasyurid	0.445	0.7223	Nil
Rodent	0.379	0.7684	Nil
Other mammal	0.300	0.8252	Nil
Passerine bird	0.931	0.4359	Nil
Non-passerine bird	2.034	0.1270	W/Sp, Sp/Su
Large insects	4.630	0.0079	W/Su, Sp/Su, (A/W)
Coleoptera	18.641	0.0006	Su/A, Su/W, Su/Sp
Orthoptera	4.428	0.0410	Su/Sp, A/Sp
Hemiptera	0.629	0.6162	Nil

regression model that incorporated macropod, arboreal and terrestrial small mammal items per scat, but omitted other mammal and reptile items per scat (adjusted R^2 = 0.597; ANOVA $F_{3,15}$ = 9.904, P = 0.0008; regression coefficients: macropod items per scat 0.184, P = 0.0332; arboreal items per scat – 0.378, P = 0.0212; terrestrial small mammal items per scat –0.919, P = 0.0026). These analyses suggest that quolls relied on scavenging significantly more when eating macropods and lagomorphs (and possibly echidnas) than when eating small dasyurids and possums or gliders.

Discussion

The present study investigated contents of scats picked up on latrines, rather than scats from trapped quolls. Thus, unlike Glen and Dickman (2006*a*, *b*), who trapped quolls in Marengo State Forest, north-eastern NSW, we could not associate individual scats with individual quolls, were unable to relate diet to the sex or age of quolls, and felt unable to rely on diameter of scat as an indicator of size and age of quoll (cf. Belcher 1995). Moreover, we sampled the same latrines repeatedly, so were probably resampling from a small number of individual quolls. Kruuk and Jarman (1995) showed that, in 1991, at least five individual quolls of both sexes (both adults and independent young) visited the area containing the set of latrines sampled in our study 7–11 years earlier. Removal of scats did not lead to a diminution through time in the numbers of scats deposited on the set of latrines, so our collection method appeared not to deter animals from using latrines.

These analyses of scats support previous reports (Alexander 1980; Belcher 1995; Jones and Barmuta 1998; Glen and Dickman 2006*a*) that the spotted-tailed quoll eats a wide range of animal foods. Plant matter was uncommon enough to have been accidentally or secondarily ingested. As in other studies, the majority of items in scats were from vertebrates; and of those vertebrate items, 61% were from mammals. Among the invertebrate occurrences, at least 42% were from insects.

In the study area quolls, while capable of eating all the locally represented classes of vertebrates, show a strong propensity for eating mammals, as in other studied populations (Alexander 1980; Belcher 1995; Jones and Barmuta 1998; Glen and Dickman 2006*a*). At least 20 genera of mammals were identified in the scats, a similar number to those identified in New England National Park, NSW (Alexander 1980) and Marengo State Forest, NSW (Glen and Dickman 2006*a*) and rather more than in Tasmania (Jones and Barmuta 1998) or northern Victoria (Belcher 1995). However, the proportion of items that were derived from mammals was lower in this study than in others (45% *v.* 89% in New England NP, 73% in Marengo SF and 71% in East Gippsland). Scats of Tasmanian spotted-tail quolls studied by Jones and Barmuta (1998) contained 81% mammalian items by percentage biomass, with male quolls voiding scats containing 90% and females 62% mammal items; the remainder of their contents was (with the exception of one crayfish) made up of bird items.

Besides containing mammal items, quoll scats in the present study contained a greater range of other vertebrate classes than in other studies. The scats we analysed were exceptional in containing frog remains (albeit rarely) and fish remains (at times abundantly), and the proportion of items from reptiles was higher than recorded elsewhere. Quoll scats found in the present study were more likely to contain arthropod remains than those from studies conducted in Tasmania, Victoria and Marengo SF, NSW (Jones and Barmuta 1998; Belcher 1995; Glen and Dickman 2006*a*). These differences between populations support the idea of quolls as opportunistic and flexible carnivores, responding to local availability of foods.

Many items detected in our study were from water-associated animals: waterbirds such as ducks, rallids, herons and cormorants; fishes; frogs; gastropod and bivalve aquatic molluscs; and yabbies. We have no evidence that the local quolls are amphibious predators; indeed, the eels and aquatic molluscs appeared in scats when eels were stranded in pools, and when falling water level exposed mussel-containing mud. Yabbies have also been found as occasional diet items in the studies in New England National Park, NSW (Alexander 1980), Marengo State Forest, NSW (Glen and Dickman 2006*a*) and Tasmania (Jones and Barmuta 1998). However, our findings do suggest that the quolls that used the latrines along the river also foraged at times along or near the riverbed.

The sizes of mammals whose remains were detected in scats in this study (like those in other studies) ranged from mice to cattle, with the majority of items coming from macropods. Scats contained remains of all wild mammals known to occur at the site except dingos and koalas, although bat remains in scats were very rare. Clearly, the quoll is not narrowly specialised in the mammals it eats, consuming species that are terrestrial and arboreal, small and large. The mammals eaten included some too large to have been killed by the quolls, and the association of fly larvae with the remains of macropods and lagomorphs (and perhaps echidnas) in the scats suggests that some larger mammals had been scavenged, while arboreal mammals, small dasyurids and perhaps rodents were less likely to have been scavenged. The gorge carries moderately dense populations of brush-tailed rock-wallabies, swamp wallabies and common wallaroos, and carcases of rock-wallabies and swamp wallabies were known to be present in the gorge in some months when those items occurred in scats (L. R. Allen, P. J. Jarman and S. W. Green, pers. obs.). Brown hares, cattle, sheep, and possibly rabbits are absent from the gorge, and their presence in the scats indicates that the quolls were scaling the 200-m walls of the gorge to forage in neighbouring pastures (where they would also have found eastern grey kangaroos).

Spotted-tailed quoll in Tasmania have been seen (M. E. Jones, pers. comm.) catching and killing adult red-bellied pademelon (*Thylogale billardieri*), which are as large as some adult brush-tailed rock-wallabies, and larger than the early young-at-foot of any of the macropods at the study site. It is therefore not impossible that quolls were obtaining some proportion of their macropod items by hunting.

The occurrence of fly larvae on carcases varied seasonally, so we may have substantially underestimated the extent of scavenging by quolls in seasons when fly activity is low.

Phalangeroid items were as frequent in the scats in this as in other studies. Phalangeroid remains constituted 73% of all items and occurred in 90% of spotted-tailed quoll scats from the high-rainfall forests of New England National Park; common ringtail possums formed 70% of phalangeroid items in New England NP, NSW (Alexander 1980). In the eucalypt forests of Marengo

SF, four identified species of phalangeroids contributed 28.5% of all food items, and greater glider (*Petauroides volans*) constituted 63.5% of those phalangeroid items (Glen and Dickman 2006*a*). In our study, brush-tail possum remains (almost certainly only *T. vulpecula*) formed 75% of phalangeroid items. Like Alexander (1980), we also identified remains of *Petaurus*, *Petauroides* and *Acrobates* species in the scats, but not of the koala. In East Gippsland, Victoria, arboreal mammals provided 23% of items in scats, and included six phalangeroid species and the tuan (*Phascogale tapoatafa*). Common brushtail possum (50% of arboreal items) and ringtail possum (29%) were the most abundant of those arboreal items (Belcher 1995). In the New England NP sample, 38% of 56 phalangeroid items were from gliding species (Alexander 1980), in Marengo SF, 64% of 178 phalangeroid items were gliders, in East Gippsland only 5% of 119 phalangeroid items were gliders; and in our sample, 15% of 189 phalangeroid items were gliders. At these sites, spotted-tailed quolls obtain a high proportion of their food items from arboreal marsupials, including ones that rarely walk on the ground. Carcases of arboreal marsupials are not frequently seen at the Dangar's Gorge site (P. J. Jarman, pers. obs.), and the implication seems to be that the quolls are adept arboreal predators. Yet data collected by Glen and Dickman (2006*b*) from radio-tracked and spooled quolls suggests that quolls rarely climbed, although the animals spent much time off the ground on logs.

Any arboreal ability quolls display does not lead to heavy predation on birds. Avian items were infrequent in our sample (7% of all items), the Marengo sample (5% of all items) and the New England NP sample (4%), but slightly more common in East Gippsland (12%). All bird items in the New England NP study were passerine (Alexander 1980), but these formed only 40% of assignable bird items in ours. Large, water-associated birds, ducks, rallids, cormorants and herons, formed 56% of bird items in our study, which is appropriate for samples from a river gorge.

In our sample of analysed scats the invertebrate items were dominated by insects (as in most other studies). Other detected large invertebrates, such as spiders, centipedes and millipedes, crustacea, and molluscs, were rare in the scats. The orders of insects were unevenly represented. Apart from an occasional ectoparasite, and items ingested with scavenged remains, the insect items were dominated by three orders of potentially large insects: Coleoptera (beetles), Hemiptera (including the cicadas), and Orthoptera (including cockroaches, crickets, and mantids). These large insects varied seasonally in their frequency in the scats, being abundantly represented in summer and early autumn (January–March) and almost absent in winter (June and July), a pattern that reflects their activity in the field. In his New England National Park study, Alexander (1980) also found insect remains much more frequently in spring (63% of scats) and summer (100% of scats) than in winter (June, July and August samples all had insects in less than 6% of scats). In their Marengo SF samples, Glen and Dickman (2006*a*) found insect items (dominated by beetles and cicadas) most abundantly in spring and summer. Beetles in our study area are particularly abundant in summer when Christmas beetles (Scarabeidae, mainly *Anoplognathus* spp) emerge and feed in thousands upon eucalypts (P. J. Jarman, pers. obs.). If they are to be eaten by quolls at all, it is unsurprising to find them most abundant in scats in summer. Almost all beetles were eaten as adults, suggesting that spotted-tailed quolls do not dig for beetle larvae.

Jones (Jones and Barmuta 1998) has shown, and Belcher (1995) has inferred, that subadult and small adult quolls are more likely than fully adult (and particularly adult male) quolls to take small prey items, including insects. Glen and Dickman (2006*a*) found insignificant trends in that direction, too. Thus our observation of abundant large insects in scats in summer may reflect the presence of juvenile animals in the quoll population in that season. Of course, the seasonal coincidence of juvenile quolls with abundant large insects upon which they may prey makes evolutionary sense, too.

Glen and Dickman (2006*a*) suggested an inverse relationship between insects and mammal items in quoll diet, but without statistical verification. In the years 1982–1984, in monthly samples when large insects were most frequent in the scats, rodents and small dasyurid items were least frequent, and vice versa. Whether this inverse relationship arises from prey switching, with quolls turning to rodents and small dasyurids when large insects become seasonally scarce, or whether this phenomenon also reflects prey switching as juvenile quolls matured to hunt larger prey, requires more direct study. Large insects were the only type of items to differ in frequency between the drought year of 1982 and the other sampled years, suggesting that scat composition reflected availability of prey as well as quoll demography. The negative relationship between reptile items per scat and arboreal mammal, rodent and large-insect items could reflect either changing diets as quolls grow or alternation between hunting tactics.

To try to understand the feeding ecology of our studied population of quolls, we sought other interactions between prey types in their frequencies in scats. The paucity of significant relationships that we found suggests that on the whole the probability that a quoll will take one type of food item is little influenced by whatever else it has found to eat. However, evidence that quolls were scavenging upon eels did coincide with decreased mean numbers of mammal and reptile remains in scats, suggesting that one abundant food source (that did not have to be hunted) displaced the normally most abundant items from the diet.

The picture of the feeding habits of the spotted-tailed quoll population that emerges from this study is of predator/scavengers that rely mainly upon mammals and large insects, are capable of hunting small and medium-sized mammals both on the ground and possibly in trees, and will frequently take vertebrate carrion (fish, fowl and mammal) when it is available. Many animal groups that are quite abundant at the study site (birds, reptiles, frogs, and several invertebrate groups) do not constitute much of the diet. However, without quantitative assessment of food-item availability we cannot comment on the quoll's dietary selectivity and preferences.

Quolls at our study site clearly sometimes foraged outside the gorge, as shown by items that are common on pastoral lands but absent from the gorge itself (lagomorphs and domestic stock). Many items in scats may derive from scavenging, although the extent to which larger species, like the macropods and lagomorphs, are actively hunted will not be known until quolls at this site are directly observed.

The spotted-tailed quoll appears to travel long distances (but well within the home-range dimensions found by Glen and Dickman 2006*b*) over steep and rocky terrain to forage away from its diurnal refuge habitat, possibly can climb trees to obtain arboreal prey items, and clearly can locate carcases. It appears to combine successfully scavenging from vertebrate carcases (especially from larger mammals), hunting arboreal and ground-dwelling smaller mammals and less often reptiles, and catching large insects, the last type of item fluctuating in seasonal occurrence in the scats.

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