Socio-seasonal changes in scent-marking habits in the carnivorous marsupial *Dasyurus maculatus* at communal latrines

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Abstract. Scat DNA analyses and monthly monitoring were used to elucidate patterns of latrine use in a free-ranging population of a rare Australian marsupial carnivore, the spotted-tailed quoll (*Dasyurus maculatus*) Kerr. In all, 132 latrines were identified at large complex outcrops and on bedrock in drainage lines, creeks and rivers at a single woodland site in south-eastern mainland Australia. Annual cyclic variation in scat deposition was found over the two years that latrines were monitored. Peaks in scat deposition on latrines coincided with seasonal social behaviours and differed between sites on outcrops and sites along drainage lines. A marked increase in scat deposition on latrines in drainage lines was recorded during the mating season and at outcrop latrines when females were nursing young. Genetic analyses of scats collected over one breeding season revealed that multiple individuals of both sexes defaecated at latrines. The communal use of latrines during the mating season along with the seasonal patterns of scat deposition demonstrates that latrines are important scent-marking sites that facilitate social communication among individuals of this solitary-living species. The collective evidence indicates that latrines play a major role in aiding reproduction and interindividual spacing.

Introduction

Scent-marking with faeces (scats), urine and glandular secretions is an important behaviour for aiding social communication in eutherian mammals (Stoddart 1976; Macdonald 1980, 1985; Gorman and Towbridge 1989) and marsupials (reviews by Eisenberg and Golani 1977; Russell 1985; Salamon 1996). The repetitive and on-going deposition of scats at landmarks is particularly common among carnivores (review by Macdonald 1985). These sites, called latrines or middens, can be used over many years and may confer information for: (1) demarcation of territories, (2) signalling ownership of resources, (3) facilitation of interindividual spacing (without territorial overtones), and (4) attracting mates by signalling sexual receptivity in females and individual presence or dominance in males (Stoddart 1976; Shorey 1977; Macdonald 1980, 1985; Croft 1982).

Latrine use has been reported in five free-ranging marsupial species: the spotted-tailed quoll (*Dasyurus maculatus*) (Alexander 1980; Belcher 1994; Kruuk and Jarman 1995), the northern quoll (*D. hallucatus*) (Oakwood 2002), the western quoll (*D. geoffroii*) (Serena and Soderquist 1989), the Tasmanian devil (*Sarcophilus harrisii*) (Pemberton 1990), and the rock-haunting possum (*Petropseudes dahli*) (Runcie 2004). However, despite some knowledge of the positioning of latrines, little is known about the participation or temporal pattern of latrine use by sex and age classes.

In the spotted-tailed quoll, accumulations of scats on prominent rocky features are reported by multiple authors (see Belcher 1994; Kruuk and Jarman 1995; Burnett 2001; Dawson 2005). However, detailed quantitative studies of sex, age and seasonal differences in scat deposition at various latrine types are required to assess the function of latrine use in this species. In this study, we combine for the first time radio-tracking, demographic and genetic analysis to investigate latrine use by the spotted-tailed quoll in detail. This complementary use of varied detection methods provides new insights into the use and social function of latrines by young and adult individuals of both sexes.

Materials and methods

Trapping and radio-tracking of quolls

This study was conducted in a 7000-ha area within the catchments of the Byadbo Wilderness Area, Kosciuszko National Park, south-eastern New South Wales, Australia. See Claridge *et al.* (2004, 2005, 2006) for detailed descriptions of the study location, topography, vegetation, climate and trapping program. Live trapping was conducted between April and July 2004–06 using

wire mesh traps ($300 \times 300 \times 600$ mm, Mascot Wire Works, Enfield South, Australia), with pairs of traps set adjacent to latrine sites. On first capture, individuals were implanted with a Passive Integrated Transponder (PIT) (Trovan Microchips Australia, Melbourne) subcutaneously between the shoulder blades, and a tissue biopsy was taken and preserved in 70% ethanol until DNA extraction. Sex was determined and age estimated based on weight (subadult ~1 year old: ♀ <1500 g, ♂ <2000 g; adults 2+ years: ♀ >1500 g, ♂ >2000 g; as per Dawson 2005).

In May 2005, radio-collars were fitted (as described in Claridge and Mills 2007) to 16 individuals: six females, nine males, and one intersexual individual (individual with pouch and penis but lacking a scrotum, XXY karyotype: Ruibal 2008). All females were regularly tracked until early July 2005 on foot during daylight (hand-held yagi antenna, Australis 26K tracking receiver, Titley Electronics, Ballina, New South Wales, Australia). This allowed locations of den sites, type of den (small or large rock complex, burrow, log, or tree hollow), and position in the landscape (creek or river, midslope, ridge) to be determined. Targeted searching for all radio-collared individuals was also undertaken and helicopter-based telemetry provided additional locational fixes on all individuals as described in Claridge and Mills (2007).

Temporal and socio-seasonal patterns of scat scent marking

A monthly monitoring survey was conducted from November 2004 to October 2006 at 132 latrines (96 creek and 36 outcrop latrines). Prior to the survey all scats were removed during August 2004, allowing a two-month re-establishment period. Subsequently, the number of new scats was monitored. Temporal changes in scat scent-marking behaviour were examined in relation to socio-seasonal periods corresponding with distinct phases of the social and breeding biology of the spotted tailed quoll, and the growth cycle of its young: (1) mating season (April–June), (2) offspring dependent (July–October), (3) offspring weaning (November–December), and (4) offspring independent (January–March).

Generalised linear models assuming a Poisson distribution with a logarithmic link function and a Bernoulli distribution with a logit link function (observed = 1, not detected = 0 for each latrine per month) were used to analyse scat deposition variation over time and season. We also categorised the latrines into two types (creek versus outcrop) to assess differences between the

latrine types. All statistical analyses were conducted using Genstat for Windows, 9th Edition (VSN International, Hemel Hempstead, UK) with statistical significance of each variable tested using deviance ratios (McCullagh and Nelder 1989).

Sex and age patterns in scat scent-marking

To elucidate sex and age patterns in scat scent-marking we matched unique microsatellite genotypes obtained from ear tissue DNA from the live-captured population against scat DNA samples collected from latrines (as detailed in Ruibal *et al*. 2009). Half of each new scat was collected at least every second day between April and July 2005 from a subset of latrines ($n = 75$). To simplify summaries we amalgamated proximate latrines (within 100 m) into 26 sites.

Results

Number of individuals identified

Over the three years a total of 52 individuals were identified, 18 females, 33 males and an intersexual individual with 23–26 individuals known per year. Typically, there were more males than females and more adults than subadults (Table 1).

Radio-tracking and den use

In the northern section of the study area, radio-collared females showed some overlap in their home ranges with other females (Appendix 1 supplied as Accessory material on the Journal's website). Males also overlapped extensively in the areas they frequented with other males and with females (Appendix 2 supplied as Accessory material on the Journal's website). Females were located by radio-tracking at 30 different den sites. All known dens were subterranean burrows, with only 13% ($n = 4$) not associated with rocks. Most dens were located on the midslope or near ridges (79%), rather than along drainage lines (21%). Across all known dens, 11 were located at or near (within 60 m) a latrine. Eight of these occurred at outcrops (six were known latrines) and three at latrines in creek lines.

Temporal and socio-seasonal patterns in scat deposition at latrines

The variation in scat deposition was broadly similar over the two years, exhibiting annual cyclic patterns (Figs 1, 2). Some temporal differences were found between the creek and outcrop latrines (Fig. 3). Temporal changes coincided with behavioural

Table 1. Summary of the trapping records per survey year and the numbers of individuals identified within each sex and age class
Also includes summary on the individuals identified via non-invasive scat and hair DNA sampling, in 2005 and 2006 respectively (Ruibal *et al*. 2010)

	2004	2005	2006
Survey dates	10–21 May, 15–25 June, 26–30 July, 16–18 Aug.	2–26 May, 4–21 July	14–18 April, 2–12 May, 4–14 July
No. of survey nights (and trapping effort)	36 (1370)	28 (1563)	26 (1408)
No. of live-trapped individuals	26 (10 ♀ : 16 ♂)	22 (6 ♀ : 15 ♂) + 1 intersexual[A]	21 (6 ♀ : 14 ♂) + 1 intersexual[A]
Additional individuals observed via non-invasive DNA	–	2 ♀, 1 ♂	2 ♂
Proportion of males	62%	67%	73%
Proportion of subadults (<1 year old)	16%	35%	32%

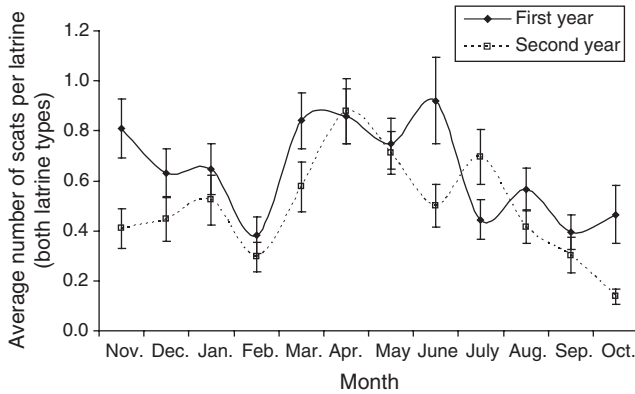[A]Individual with pouch and penis but lacking a scrotum, XXY karyotype (Ruibal 2008).

Fig. 1. Comparison of the average number (±s.e.) of scats deposited at each of the 132 latrines per month in each monitored year.
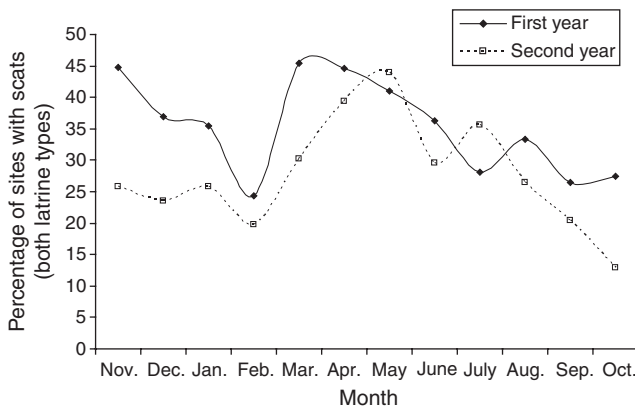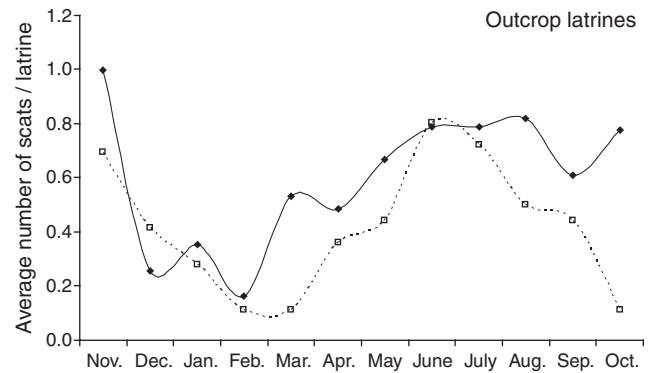

Fig. 2. Comparison of the proportion (%) at each of the 132 latrine sites with at least one scat deposited during monthly periods in each monitored year.
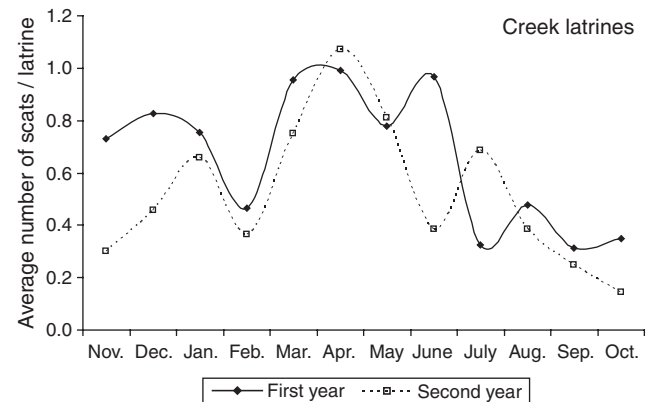

Fig. 3. Comparison of the average number of scats detected at outcrop (*n* = 36) and creek (*n* = 96) latrines in each of the monitored years. Socio-seasonal periods corresponding with the breeding biology and the growth cycle of young are shown.

changes associated with reproduction (Fig. 3). For example, deposition peaked at creek line latrines during the mating period then dropped sharply when females had pouch young. Low rates of deposition continued during the offspring-dependent period. During the offspring-independent period the rate of scat deposition declined at the outcrop latrines, but increased at the creek latrines.

Linear modelling revealed significant variation in the proportion of latrines with a scat present (Table 2) and the average number of scats deposited at the latrines (Table 3) over time, among the type of latrine, and among seasonal periods (type × season interaction). Thus the major influence of the overall variation was the type of latrine and socio-seasonal periods.

Scat deposition by individuals during the mating and post-mating period

In total, 262 scats were collected from 26 latrine sites (56 latrine platforms) over the four-month scat survey (April–July 2005). DNA was retrieved from 208 scats. Twenty-eight unique genotypes were identified; 18 matched known 2005 individuals, and two were matched to 2006 individuals. Four male adults of the 2005-trapped population were not sampled via scat

Table 2. Outcomes of generalised linear modelling of the proportion (%) of latrines observed with at least one fresh scat at the two types of latrines (creek *versus* outcrop latrines) to test for differences in scat deposition

Change	d.f.	Deviance	Mean deviance	~*F*
First year (November 2004–October 2005)				
Type	1	0.28	0.28	0.595
Season	3	16.50	5.50	**<0.001**
Month	8	16.97	2.12	**0.03**
Type × season	3	23.43	7.81	**<0.001**
Type × month	8	4.19	0.52	0.84
Residual	1441	1840.86	1.28	
Total	1464	1902.23	1.30	
Second year (November 2005–October 2006)				
Type	1	6.33	6.33	**0.012**
Season	3	25.17	8.39	**<0.001**
Month	8	31.00	3.88	**<0.001**
Type × season	3	12.56	4.19	**0.006**
Type × month	8	13.88	1.74	0.085
Residual	1560	1780.93	1.14	
Total	1583	1869.87	1.18	

Table 3. Outcomes of generalised linear modelling of the number of scats observed at the two types of latrines (creek *versus* outcrop latrines) to test for differences in scat deposition

Change	d.f.	Deviance	Mean deviance	~F
First year (November 2004–October 2005)				
Type	1	0.99	0.99	0.42
Season	3	52.16	17.39	**<0.001**
Month	8	28.69	3.59	**0.016**
Type × season	3	53.11	17.70	**<0.001**
Type × month	8	18.30	2.29	0.149
Residual	1441	2184.87	1.52	
Total	1464	2338.13	1.60	
Second year (November 2005–October 2006)				
Type	1	6.95	6.95	**0.022**
Season	3	45.27	15.09	**<0.001**
Month	8	85.66	10.71	**<0.001**
Type × season	3	38.58	12.86	**<0.001**
Type × month	8	37.69	4.71	**<0.001**
Residual	1560	2069.13	1.33	
Total	1583	2283.28	1.44	

DNA. The 20 genotypes matched to known individuals included adults ($n = 12$) and subadults ($n = 8$) of each sex (adults: ♂ = 7, ♀ = 5; subadults: ♂ = 5, ♀ = 2; and 1 subadult intersexual individual).

DNA was successfully amplified from 149 of 183 (81.4%) scats from creek latrines and 59 of 79 (74.7%) scats from outcrops over 23 latrine sites (of 26). Most (74%) latrine sites had scats from both sexes (Appendix 1). The total number of individuals using a given latrine site varied from one to seven (average 3.5) with up to six males but at most two females per site (Table 4). Males of each age cohort (subadult $n = 5$, adult $n = 7$) used latrines in most months (data not shown). Females of each age cohort (subadult $n = 2$, adult $n = 5$) used latrines each month from April until 2 July (data not shown). After this date, and until 22 July when the sampling period ceased, none of the scats collected were attributed to females. Thus, the marking strategy of females altered in July, coinciding with the birth of young (three of the four females trapped in July/August had pouch young present: M. Ruibal, unpubl. data).

Over the period when both sexes were marking, scats from females were encountered, on average, at a similar rate to those from males (mean ± s.e.: ♀ 9.1 ± 3.1, range = 2–27, $n = 8$; ♂ 8.9 ± 2.7, range = 1–37, $n = 12$). Subadults were detected more often than adults (subadult 12.1 ± 4.6, range = 1–37, $n = 8$; adults 7.3 ± 1.6, range = 2–18, $n = 12$). Among males, subadults were observed, on average, more often than adults (♂ subadult 11.4 ± 5.6, range = 1–37, $n = 5$; ♂ adults 8.4 ± 2.4, range = 2–18, $n = 7$). Scats belonging to both sexes and age classes were found at the two latrine types. On a monthly basis, the number of females detected at outcrop latrines was two or three and males four (Table 5). In contrast, at creek latrines most females were detected each month (6 or 7 females), except for July. Also, more males were detected in each month at creek latrines than at outcrop latrines (Table 5).

Discussion

Non-invasive DNA sampling of scats from latrines, in combination with a DNA and demographic database on trapped individuals has provided, for the first time, unique insights into the use of latrines by spotted-tailed quolls. All animals in the population, regardless of sex or age, used latrines, with annual cycles in the frequency of scat deposition and variation that coincided with seasonal social behaviours. It is thus evident that scats are actively used as a scent signal (under Kleiman's (1966) criteria) and latrine-forming behaviours have multiple functions. Here we use scat-deposition data to consider these possible functions.

Functional significance for reproduction

A reproductive function is widely assumed when scent-marking behaviours increase or are restricted to the breeding period (see Macdonald 1980; Gorman and Towbridge 1989). We observed a marked increase in scat deposition and the proportion of latrines used during the mating period consistent with qualitative evidence in other studies of spotted-tailed quolls (Alexander 1980; Belcher 1994; Dawson 2005), and of the northern quoll (*D. hallucatus*) (Oakwood 2002). Latrine use for reproduction by spotted-tailed quolls may function both to advertise female sexual receptivity and male presence or dominance.

Table 4. Numbers of the average and range of individuals identified from scat DNA collected between April and the end of July 2005 from single latrines (per single rock feature) and latrine sites (where several latrines occurred within an outcrop complex or <100 m of each other along a creek line)
Summaries are provided for single rock features and latrines grouped by proximity to show that an equivalent average number of individuals and range of individuals were observed with amalgamation of latrines. Also, similar numbers of individuals were observed when individuals identified solely from scat DNA were excluded. Latrines from which fewer than two scats were collected are not included

		Individuals per latrine		Individuals per site[A]	
		Average	Range	Average	Range
All individuals identified by means of scat DNA	Total ($n = 28$)	2.6[B]	1–6	3.5	1–7
Excluding transient individuals identified via scat	Females ($n = 8$)[D]	0.9[C]	0–2	1.1	0–2
DNA only once or solely in April	Males ($n = 12$)[E]	1.5[C]	0–5	1.8	0–6
	Total ($n = 21$)[F]	2.5[C]	1–6	3.0	1–7

[A]$n = 23$ sites. [B]$n = 40$ single rocks. [C]$n = 37$ single rocks. [D]Includes one unknown individual that was determined to be female given the non-amplification of *SRY* gene and amplification of a control marker (see Ruibal 2008). [E]Four adult male individuals trapped in 2005 were not identified via the scat DNA collection conducted during the same period. [F]Includes an intersexual individual not incorporated in the comparison between sexes given its ambiguous sexual identity and therefore behaviour.

Table 5. Summary of the number of scats for each sex collected at outcrop and creek latrines that yielded DNA

The number of individuals identified is shown in parentheses. The number of scats for which no DNA was retrieved at each of the latrine types is also shown

Latrine type	Sex	April[A]	May[A]	June[A]	July[A]
Outcrop	Female (n = 8)	8 (2)	3 (3)	15 (2)	0
	Male (n = 12)	0	4 (3)	19 (4)	5 (4)
	No DNA	2	6	10	3
Creek	Female (n = 8)	18 (7)	12 (7)	15 (6)	2 (2)
	Male (n = 12)	21 (7)	20 (7)	39 (8)	8 (4)
	No DNA	12	11	9	1

[A]Summaries exclude an intersexual individual and scat samples belonging to 7 individuals unknown from the trapped population, but include one unknown female individual (Ruibal 2008).

Scent marking by females may allow them to advertise their pending sexual state to attract potential mates (Clapperton 1989). The duration of female attractiveness to males varies between species but is known to begin before they enter oestrus (Ewer 1968; Russell 1984). The benefit of a prolonged preoestrous period of attractiveness, particularly in solitary species where female–male encounters are not regular, is that it ensures that males are present when females are ovulating, and thus secures mating opportunities (Ewer 1968).

The finding that all female spotted-tailed quolls used latrines in April, before litters were conceived, then ceased to mark when offspring were born suggests that this may allow females to advertise their pending sexual state to attract potential mates. If so, this would provide an efficient means for males to monitor female receptiveness, while minimising unwarranted copulations or aggression. A preoestrous period of attractiveness is also likely to enhance opportunities for polyandry. Mixed-paternity litters have indeed been revealed by paternity analysis of spotted-tailed quolls (Glen *et al.* 2009).

Scent marking by males can be used to simultaneously signal their presence to females and competing males, where dominant or larger males mark at a greater rate to signal their status (Gorman and Towbridge 1989). This could allow subordinate males to avoid confrontation with a dominant individual, while allowing females to assess mate quality (Rich and Hurst 1998; Hurst and Rich 1999; Begg *et al.* 2003). A dominance hierarchy based on size and age is thought to operate among male spotted-tailed quolls (Belcher 2000; Andrew 2005; Glen *et al.* 2009), given the roving strategy adopted by males during the mating season, evidence for polyandry and paternity analysis revealing that larger males sire more young (Croft 2003; Croft and Eisenberg 2006; Glen *et al.* 2009). However, the finding in the present study of no difference in the scat-marking frequency between adult and subadult males, and no evidence that subadult males were deterred from marking at latrines, does not concur with the dominance hierarchy hypothesis.

Functional significance for mediating spatial organisation

Since scat deposition in the spotted-tailed quoll occurs throughout the year, latrines must have other functions beyond a reproductive

role. Our finding that scat deposition by both sexes was greater at creek than outcrop latrines during the mating period suggests that individuals made strategic decisions about scat placement to maximise discovery. The low relief and linear configuration of creeks and rivers in the study area may assist the efficiency of the roving strategy of males. Accordingly, females too would maximise the number of potential sires by scent-marking more often in areas where several males may be encountered. Latrines occurring on linear features (paths and river crossings) were also more heavily used by the western quoll, leading Serena and Soderquist (1989) to postulate that these were places where animal movements were likely to be concentrated.

In contrast to creek latrines, peak scat deposition at outcrop latrines occurred during the offspring-dependent period, often in proximity to known den sites. Therefore, scat deposition at outcrops during this period may function to advertise female occupancy of dens. The protection and exclusive use of limited resources (such as dens and food) is the motive invoked for female territoriality in all three quoll species (Serena and Soderquist 1989; Oakwood 2002; Belcher and Darrant 2004; Andrew 2005). However, given our finding that more than one female may scent mark at a latrine and that females with adjacent or overlapping home ranges are often closely related (Ruibal 2008), scent-marking may instead operate as a form of 'social book keeping' that enables females to keep track of related individuals and so maintain social cohesion. Females may also scent mark to aid their offspring's familiarisation with the natal area once their young make excursions outside the den and young may also begin to mark for the same purpose.

This study has confirmed for the first time that spotted-tailed quoll latrines are communal areas at which subadults and adults of each sex participate in scent-marking behaviours. Furthermore, we have shown that patterns of deposition vary both seasonally and in relation to the spatial location of latrines. These patterns indicate that latrines provide focal areas to exchange information for reproductive purposes, by attracting or seeking mates, and more generally for maintaining interindividual spacing. Finally, this study demonstrates the power of combining genetic analyses with observational and demographic data to gain greater insights into the significance of latrine-forming behaviours in an otherwise cryptic species.

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