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Scats can reveal the presence and habitat use of cryptic rock-dwelling macropods

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Abstract. The rock-dwelling macropod species of the tropics of the Northern Territory, Australia, are behaviourally elusive and difficult to observe in their rugged habitats. Hence, little is understood about their ecology. We evaluated the potential of using scats (faecal pellets) as a survey tool for this faunal assemblage by: (1) developing a key to the scats of the species; (2) examining the rates of loss and decomposition of short-eared rock-wallaby (*Petrogale brachyotis*) scats in these tropical environments; and (3) comparing the distribution of scats of *P. brachyotis* with the species' use of space and habitats as determined with radio-telemetry. Classification tree modelling discriminated the scats of the seven macropod species, primarily on the basis of width. The reliability of identification was greatly improved with larger sample sizes and inclusion of a habitat parameter. Rates of scat loss and decay were variable and the greatest losses occurred in the wet season, particularly on sandy soils. Scat censuses underestimated the total area used by *P. brachyotis* but the distribution of scats showed the same broad pattern of habitat use found by radio-telemetry. We conclude that scats can accurately indicate the presence and habitat preferences of rock-dwelling macropod species.

Introduction

Spoor, particularly scats (faecal pellets), has been widely used by indigenous peoples and hunters to identify the presence and location of animals. Ecologists and land managers have also favoured using scats to study wildlife populations because it is a non-intrusive technique and far less labour intensive than traditional methods such as mark–recapture or behavioural observations (Putman 1984; Kendall *et al.* 1992; Webbon *et al.* 2004). Scats have been used in surveys of a range of taxa, including ungulates and carnivores (e.g. Neff 1968; Komers and Brotherton 1997; Bonesi and Macdonald 2004). In Australia, the technique has provided insights into the ecology and behaviour of various macropod species (e.g. Caughley 1964; Hill 1981a; Lunney and O'Connell 1988; Banks 2001).

The successful use of scats in ecological studies of macropods suggests that they may be an ideal tool for investigating the cryptic rock-dwelling macropods of the monsoon tropics of northern Australia. The rock-dwelling macropods of the region (*Petrogale brachyotis*, *P. concinna*, *Macropus bernardus* and *M. robustus*) inhabit steep rocky terrain and flee to shelter when disturbed. The physical environment and their wary behaviour present formidable challenges to ecologists, and little is known about their ecology (Strahan 1995). It remains uncertain whether scats can be used effectively to collect information about these species. Recent advances in DNA analysis of scats offer great accuracy in determining the presence of species; however, for the rock-dwelling macropod species of northern

Australia that inhabit such rugged, remote areas, a relatively efficient technique that does not depend on preservation of DNA is required.

There are several critical assumptions that underpin the use of scats in surveys. First, the scats of the species must be identifiable from other sympatric species. This is possible for many macropod species in Australia whose scats have a characteristic and distinct shape (Triggs 1996; Jarman and Capararo 1997). However, high rates of identification error sometimes occur. For example in a Tasmanian study, all observers, including those who frequently identified scats in the field, sometimes incorrectly identified Bennett's wallaby (*Macropus rufogriseus*) and pademelon (*Thylogale billardieri*) scats (Bulinski and McArthur 2000). The scats of the macropods of the Northern Territory have received little attention. Triggs (1996) offers photographs and broad size categories for some species, and Churchill (1997) suggests that scats of *P. concinna* and *P. brachyotis* are distinguishable but does not describe how. Thus it remains unclear whether the scats of the sympatric species can be reliably identified.

If scats are used to determine habitat preference and monitor changes in site occupancy of species, it is important to determine whether the loss of scats is equal across habitats and between seasons (Perry and Braysher 1986; Southwell 1989). Two processes affect the persistence of scats: decay occurs *in situ* by physical weathering and insect activity, and loss of scats occurs by factors such as water run-off, wind, fire and removal by invertebrates. Experiments have found

that environmental conditions and substrate greatly affect scat longevity. For example, scats persist much longer in cool, dry conditions and disappear rapidly in warm, wet conditions (Harestad and Bunnell 1987; Johnson and Jarman 1987; Vernes 1999). Also, scats deposited on rocks and in caves may dehydrate quickly and decay slowly (Jarman and Capararo 1997), and those in long grass decay more quickly than those in short grass (Johnson and Jarman 1987). Most studies of persistence have tended to be short-term (1–3 months: Johnson and Jarman 1987; Vernes 1999) and, therefore, investigation of the rates of loss and decay of scats over the course of a wet- and dry-season cycle in the monsoonal tropics is warranted.

When scats are used in surveys of habitat use and foraging range, it is often assumed that the density and distribution of scats faithfully reflect the daily and seasonal movement patterns of the species. In the case of macropods, defaecation has been observed to occur frequently while feeding and infrequently while resting (Hill 1978; Johnson *et al.* 1987). Thus the density and distribution of scats have primarily been interpreted as showing which habitats are used by macropod species for feeding (Caughley 1964; Hill 1981b; Lundie-Jenkins 1993). However, there has been little detailed examination of the concordance between the distributions of scats and the activity patterns and foraging ranges of macropod species. Studies in North America have found that the distribution of deer pellets underestimated their use of some habitats as determined by observation or radio-telemetry (Collins and Urness 1981; Loft and Kie 1988). Clarification of the relationship between the distribution of scats and a species' use of space and habitats is therefore required before the techniques are employed to study the habitat use of the macropod species.

This research provides the background information required to use scats as a tool to study the rock-dwelling macropods of the monsoon tropics of the Northern Territory, Australia. To specifically address the above assumptions, we examined the following three questions. (1) Can scat morphometrics of the seven macropod species in the tropics of the Northern Territory be used to reliably distinguish between species? (2) Is the rate of loss and decomposition of

short-eared rock-wallaby (*Petrogale brachyotis*) scats different between seasons and among substrates in these tropical environments? (3) How does the spatial distribution of scats of *P. brachyotis* compare with the species' use of space and habitats determined by radio-telemetry?

Methods

Scat identification key

We collected scats from seven macropod species found in the tropics of the Northern Territory (Table 1) from areas where the identification of the scats was known (from direct observation, previous studies and/or local knowledge). Scats of the rock ringtail possum (*Petroseudes dahli*) were also examined as this species is commonly found in the rocky habitats used by the rock-dwelling macropods. Although we recognise that there is some circularity in assuming that scats found in the wild came from a particular species, this offered the only feasible methodology since some of the species of interest are not held in captivity, nor are they trappable. Furthermore, scats of animals in captivity that are fed on vegetable diets are often quite different in size and shape to those of wild animals. For example, we found that the scats of some species such as agile wallabies (*M. agilis*) held at the Territory Wildlife Park were quite different in size and shape to scats collected from wild animals from the population of *M. agilis* at East Point Reserve, Darwin.

Between 35 and 500 scats per species were measured depending upon the availability of scats, with 2300 scats measured in total. We measured the size dimensions (length, width and breadth) of each scat with calipers to an accuracy of 0.1 mm (Fig. 1). We also recorded colour (black, brown, fawn, grey, white or rufous), shape (square, round, rectangular, heart- or tear-shaped), and the presence of 'squeeze points' (thin taperings at the end of scats: Fig. 1). A scat identification key was developed using Classification Tree modelling (Breiman *et al.* 1984; Feldesman 2002) in the software package R (version 2.0.1, R Development Core Team). Classification trees use binary recursive partitioning to predict sample membership in the classes of a categorical response variable (macropod species) from measurement of explanatory variables (size, shape, colour and presence of squeeze point). A maximum of 200 scats per species was included in the analysis so that the variances around the means of the samples were more comparable. We first ran the model with scats of all species, and then re-ran the model with only scats of the four rock-dwelling macropod species to examine the accuracy of identifying scats found solely in rocky habitats.

Scat-persistence experiment

We investigated the effects of substrate and season on the rate of decomposition and persistence of scats in the monsoon tropics in an experiment run over 2 years at Litchfield National Park (13°07'S, 130°48'E). Like the rest of the monsoon tropics in northern Australia, this region

Table 1. Size characteristics and collection locations of the scats of the seven macropod species and the rock ringtail possum (*Petroseudes dahli*) in the monsoon tropics of the Northern Territory

Species	No. scats measured	Length (mm)		Width (mm)		Breadth (mm)		Location of collection	
		Mean	Range	Mean	Range	Mean	Range	Latitude	Longitude
<i>Macropus agilis</i>	500	22.7	11.5–41.8	15.9	10.7–25.8	12.4	8.7–21.1	12.413°S	130.830°E
<i>M. antilopinus</i>	180	24.9	11.1–41.5	20.1	11.5–28.3	15.7	10.5–22.4	13.180°S	131.310°E
<i>M. bernardus</i>	300	24.7	13.4–38.6	19.9	11.9–28.5	14.5	7.8–20.9	12.768°S	133.839°E
<i>M. robustus</i>	140	24.2	14.5–35.9	22.9	12.5–30.5	16.1	10.0–19.8	13.215°S	130.744°E
<i>Petrogale brachyotis</i>	500	17.1	7.0–32.4	10.5	5.5–14.5	8.6	4.2–17.8	13.126°S	130.815°E
<i>P. concinna</i>	100	10.3	6.9–14.3	8.7	6.1–12.0	7.1	4.4–9.7	12.060°S	132.884°E
<i>Onychogalea unguifera</i>	35	20.4	11.1–37.3	12.3	7.0–19.0	10.4	5.8–14.5	13.127°S	131.372°E
<i>Petroseudes dahli</i>	120	18.0	13.5–25.8	7.0	5.4–8.9	6.6	3.8–8.5	12.377°S	132.936°E

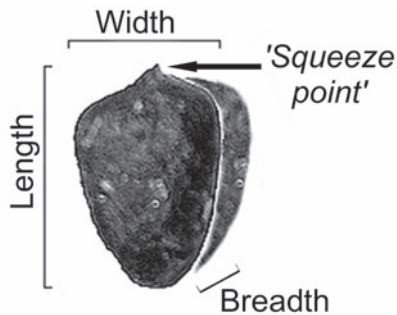


Fig. 1. Characteristics of scats measured for the scat-identification key.

has a strongly seasonal distribution of rainfall (100–600 mm per month in the wet season, December–April, versus <10 mm per month in the dry season, May–September: Bureau of Meteorology, Darwin). Another characteristic of the environment in the region, including at the sites of this study, is landscape fire, which occurs frequently in the dry season (Edwards *et al.* 2001).

In September 2002 (before the onset of the wet season), we established groups of four replicate 1 × 1 m quadrats on two substrate treatments (rock and litter over sand) at four spatially separated sites (over a distance of 15 km). This experimental design maximised the chance of some sites escaping being burnt in the dry season and captured local variation in substrate conditions. To ensure that no new scats were deposited within the quadrats, we situated quadrats on outcrops and in adjacent sandy areas where there were no existing scats or signs of rock-wallaby presence. However, care was taken to choose sites where the conditions present were as similar as possible to those where rock-wallabies are present. We reset the experiment in the dry season of 2003 at one site, with eight replicates on each of the two substrates, to examine the decay and loss of scats starting in the dry season (the first experiment is referred to as ‘Experiment A’ and this later one as ‘Experiment B’).

In both experiments, we positioned 15 fresh short-eared rock-wallaby (*Petrogale brachyotis*) scats, collected from a nearby site, within each quadrat. Every 2 months, the number of scats remaining and the condition of the scats were recorded. The condition of the scats was visually characterised in six categories based on colour, proportion of light-coloured fibres visible and condition of the surface of pellets (as listed in Table 2). The presence of insect damage was also recorded.

Changes in the condition of the scats with both time and substrate were examined using descriptive statistics, and *t*-tests were used to examine the effect of substrate on the persistence of scats (number of scats completely gone) in each condition category. The effect of different substrates on the loss of scats over time was analysed using repeated-measures analysis of variance.

Spatial distribution of scats

We compared how well the distribution of scats indicated the use of space and habitats of short-eared rock-wallabies with that found using radio-telemetry from a concurrent study. Eight *P. brachyotis* were radio-tracked in June and July 2003 at a 100-ha site at Litchfield National Park (documented in detail in Telfer and Griffiths 2006). In that study, fixes (locations of the animals at any particular time) were obtained both nocturnally and diurnally, and used to determine the use of space and habitat by *P. brachyotis*. Since the tagged animals are estimated to be only ~15% of the population at the site (Telfer and Griffiths 2006), the fixes represent the activity of only a small portion of the total activity of the population. Hence, the distribution of scats was expected to be greater than the area covered by the fixes.

Across the study site where the radio-tracking study was conducted, we measured the density of *P. brachyotis* scats in a 1-m² quadrat at points of a 100-m lattice (located using a global positioning system) in August 2003. Scat densities were attributed to four categories: none, low (1–2 scats), medium (3–6 scats) and high (≥7 scats). For each quadrat we also estimated the following environmental variables: habitat type (outcrop, flat adjacent to outcrop, hill slope, hilltop, and swale), percentage cover of rock, presence or absence of grass, and whether the area had been burnt.

We estimated the coverage of scats and habitats across the site from the classification of the site into the 100 × 100-m cells of the lattice. The influence of environmental variables on the density of *P. brachyotis* scats was measured using generalised least-squares (GLS) modelling. To overcome the inherent spatial autocorrelation in the study design we first examined a range of geostatistical autocorrelation models (spherical, ratio, linear, Gaussian and exponential) to determine which model best fit the spatial patterning of our data (Keitt *et al.* 2002). These models account for spatial patterning by modelling the correlation between errors directly as a function of distance (Keitt *et al.* 2002). We ran each autocorrelation function with a GLS of the global model and used Akaike’s Information Criterion (AIC: Burnham and Anderson 2002) to rank the models. There was little difference in the AIC values and Akaike weights between the different geostatistical autocorrelation models, but the lack of support for the global model run without an autocorrelation correction showed that it was important to use one of the corrections in the analysis. Thus we subsequently used GLS with a linear correlation function to analyse a set of candidate models to determine which environmental variables were correlated with scat density. The candidate model set included univariate models of the variables ‘habitat’, ‘burnt’ and ‘rockiness’, and other combinations of these variables (Table 3). Presence of grass was highly correlated with ‘burnt’ so was excluded from the analysis. The candidate models were ranked using AIC_c (the second order form of Akaike’s Information Criterion used for small sample sizes) to determine the best model.

Determining habitat preferences using traditional χ^2 tests has commonly been criticised as being biased due to pooling across individuals and non-independence of samples and habitat proportions (Aebischer

Table 2. Categories of scat condition used in measurement of persistence and decay of *Petrogale brachyotis* scats in experiments at Litchfield National Park

Category	Description
1	Shiny black or dark brown, dried mucous coating still present, pellets firm and no signs of breakdown; sand particles may be adhering to pellets
2	Matte black/brown, pellets firm and no signs of cracking or breakdown
3	Dull black/brown, 0–25% light-coloured fibres showing, cracking
4	Dull black/brown, 25–50% light-coloured fibres showing, cracking
5	Patchy dull black to grey, 50–75% light-coloured fibres showing, weathered appearance
6	Generally dull grey, 75–100% light-coloured fibres showing, weathered appearance and often crumbly to touch
7	Signs of insect damage visible, or half eaten

Table 3. Model selection results of generalised least-squares models of density of *Petrogale brachyotis* scats and influence of habitat variables at Litchfield National Park

$\text{Log}(L)$ is the maximised log-likelihood of the model, K is the number of estimated parameters, AIC_c is the selection criterion, ΔAIC_c is the difference between the model's AIC_c value and the minimum AIC_c value, and w_i is the Akaike weight. The candidate model with a significant level of empirical support ($\Delta\text{AIC}_c < 2$) is shown in bold

Number	Candidate model	$\text{Log}(L)$	K	AIC_c	ΔAIC_c	w_i
1	Habitat	-108.40	5	227.33	0.00	0.84
2	Habitat + burnt	-109.18	6	231.09	3.76	0.13
3	Habitat + rockiness	-110.65	6	234.04	6.71	0.03
4	Rockiness + habitat + burnt	-111.43	7	237.85	10.52	<0.00
5	Rockiness	-129.01	2	262.13	34.80	<0.00
6	Rockiness + burnt	-129.58	3	265.36	38.04	<0.00
7	Burnt	-139.41	2	282.91	55.59	<0.00

et al. 1993). Thus, Telfer and Griffiths (2006) used compositional analysis (Aebischer *et al.* 1993) to rank the habitat preferences of *P. brachyotis* determined using radio-telemetry. In the present study, we compare the ranking of the regression coefficients of the GLS model of how scats represent the use of habitats, with that found in Telfer and Griffiths (2006), namely: outcrop > flat > hill slope > swale > hilltop.

For diagrammatic representation, scat density was smoothed using regularised spline interpolation (12 nearest-neighbour points with a weighting of 0.1) in ArcMap with Spatial Analyst (version 9.0; ESRI, Redlands, CA, USA).

Results

Scat identification key

The size and shape of scats varied greatly within and between individuals of each species (Table 1). Nonetheless, there were sufficient differences in the scats of each species to enable their identification and separation into a key (Fig. 2). Scats of *P. brachyotis* and *P. concinna* (the rock-wallaby species) and the rock ringtail possum (*Petroseudes dahli*) were first separated from the scats of the larger *Macropus* species on the basis of width. Rock-wallaby scats were small (generally <14 mm in width) and black to brown in colour, and were separated from the scats of the rock ringtail possum, which are usually more rufous in colour. Nabarlek (*P. concinna*) scats were separated from those of the short-eared wallaby (*P. brachyotis*) by their shorter length (generally <12 mm).

The classificatory process separated the scats of the agile wallaby (*M. agilis*) from those of the other *Macropus* species on the basis of their lesser width (<19 mm), and *M. robustus* scats from those of *M. bernardus* and *M. antilopinus* by their greater width (>24 mm). The scats of these latter two species were separated by shape: scats of *M. bernardus* tended to be more heart-shaped, whereas those of *M. antilopinus* were predominantly rectangular. Scats of the northern nailtail wallaby (*Onychogalea unguifera*) tended to be smaller and more cylindrical than those of the *Macropus* species but, due to the low number of scats available, the classification modelling did not separate scats of this species from those of the other macropod species.

In the model of all of the macropod species, the overlap in the size and shape of the scats of many of the species (Table 1) caused a high misclassification error rate (31.9%). For example, the scats of young *P. brachyotis* were often indistinguishable from those of *P. concinna*, and many scats of the different *Macropus* species were also indistinguishable. When scats of only the rock-dwelling macropod species (*M. bernardus*, *M. robustus*, *P. concinna* and *Petrogale brachyotis*) were included, the model classified the species using the same explanatory variables (Fig. 3) but had a much lower misclassification rate (14.8%). This misclassification rate is based on prediction of any one scat, so species prediction will be reasonably accurate when a greater number of scats are measured.

No species were classified in the key on the basis of the presence or absence of 'squeeze points', which were a common

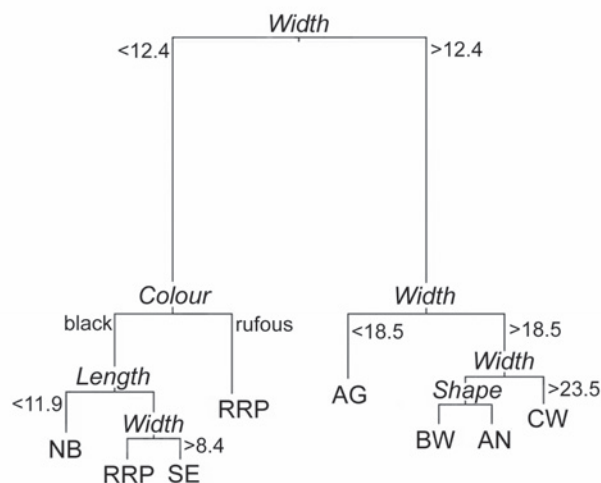


Fig. 2. Classification tree model of the scats of the macropods and associated species of the monsoon tropics of the Northern Territory. AG, agile wallaby (*Macropus agilis*); AN, antilopine wallaroo (*M. antilopinus*); BW, black wallaroo (*M. bernardus*); CW, common wallaroo (*M. robustus*); NB, nabarlek (*Petrogale concinna*); RRP, rock ringtail possum (*Petroseudes dahli*); SE, short-eared rock-wallaby (*Petrogale brachyotis*). Scat measurements are in millimetres.

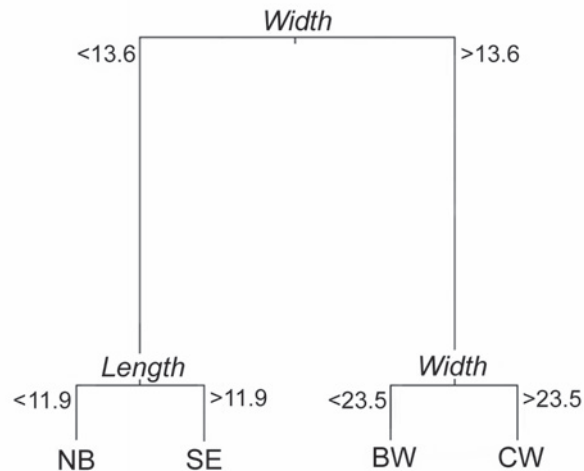


Fig. 3. Classification tree model of the scats of the rock-dwelling macropods of the monsoon tropics of the Northern Territory. BW, black wallaroo (*Macropus bernardus*); CW, common wallaroo (*M. robustus*); NB, nabarlek (*Petrogale concinna*); SE, short-eared rock-wallaby (*Petrogale brachyotis*). Scat measurements are in millimetres.

characteristic across scats of the macropod species (42–58% of those sampled) but uncommon in rock-ringtail possum scats (4%). Although not used in developing the key, texture and density of scats can also assist identification. All the macropod scats had a fibrous texture in contrast to the finer texture of the scats of the rock-ringtail possum and other small mammals. Scats of *P. brachyotis* and *M. bernardus* were usually found in high densities as a result of these species' sedentary use of rocky shelters and the high densities of animals in the vicinity of these rocky areas (personal observations).

Scat-persistence experiment

In both experiments a large proportion of *P. brachyotis* scats were lost in the first 6 months (54.4% of all scats in

Experiment A and 59.2% in Experiment B). Yet, surprisingly, some scats persisted for over 2 years (Fig. 4). In general, scats lost their black exterior and more light-coloured fibres became visible with time. 'New' scats appeared black/brown and glossy (Category 1) for up to 4 months (Fig. 5). However, 'old' scats (grey and fraying) may be anything between 2 and >24 months old. After 2 years nearly all scats appeared 'very old' (grey, crumbling to touch, 75–100% fibres visible).

The greatest losses of scats occurred in the wet season (December–March) and there was also substantial destruction of scats by fires in the dry season (Fig. 4). There was a significant effect of substrate on the rate of loss of scats (Experiment A: $F_{1,30} = 5.270$, $P = 0.029$; Experiment B: $F_{1,14} = 4.932$, $P = 0.044$). In both experiments more scats were lost over a shorter period from plots with litter over sand than from those on rocky substrate.

Decay of scats also occurred more slowly in the dry season than in the wet season, and scats decayed and aged more rapidly on rocky plots than on sandy plots with litter. Scats persisted significantly longer in Category 2 (black and matte with no cracking) in sandy than in rocky plots (Experiment A: $t_1 = 3.667$, $P = 0.001$) and significantly longer in Category 6 (grey, 75–100% fibres visible) on rock than in sandy plots (Experiment A: $t_1 = -4.018$, $P < 0.001$). Substrate did not significantly affect the persistence of scats in all other categories, including Category 7 (insect damage).

Spatial distribution of scats

Generalised least-squares analyses with AIC_c model selection indicated that habitat was the best model of scat density, with an 84% probability of being the best model of the candidate set (Table 3). There was little support for other models that contained the variables burnt and rockiness. The standardised regression coefficients of the habitat model showed

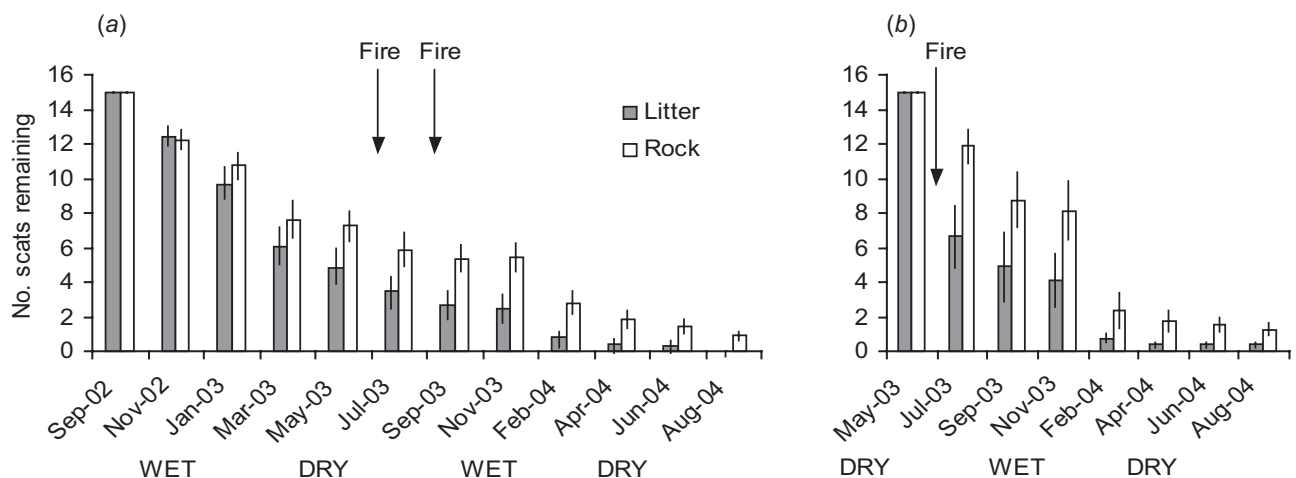


Fig. 4. Loss of scats per plot with time and substrate in (a) Experiment A starting in September 2002, and repeated in (b) Experiment B starting in May 2003 (means \pm s.e.) at Litchfield National Park. Fifteen fresh scats were initially positioned within each plot.

that, of the different habitat types, outcrop had the highest *P. brachyotis* scat densities, followed by the flat adjacent areas, the hill slope, swale and the hilltop. Thus scat densities indicated the same ranking of the use of habitats as was found with radio-telemetry: outcrop > flat > hill slope > swale > hilltop. However, in contrast to the telemetry results, these coefficients and their 95% confidence intervals suggested that there was significantly greater use of the outcrops than other habitats, and less obvious differences in the use of the flat areas, hill slope and swale (Fig. 6). Thus there were some fine-scaled differences in the use of habitats described by the two techniques.

Scat densities were not strongly associated with the locations of all fixes of *P. brachyotis* (Fig. 7). Many fixes were in areas with no scats present (21.1%) and in areas with low scat densities (32.9%). However, scats were strongly associated with diurnal fixes (resting and den sites): scats were always present where there were diurnal fixes. In general,

high densities of scats were found on outcrops and scats decreased in density with distance from these areas.

Discussion

The three experiments of this study showed that scats can be used effectively to survey cryptic species such as the rock-dwelling macropods of the monsoon tropics. In the following discussion we describe how scats can be used most accurately in surveys of distribution and habitat use of these species, and to monitor their ongoing presence at sites. We primarily discuss the case study of the short-eared rock-wallaby (*P. brachyotis*) but also extend the discussion to the rest of the rock-dwelling macropod assemblage found in the tropics of the Northern Territory, Australia.

Surveying distribution

Scats of *P. brachyotis* were the most distinctive of the seven macropod species in the region. They could be easily distin-

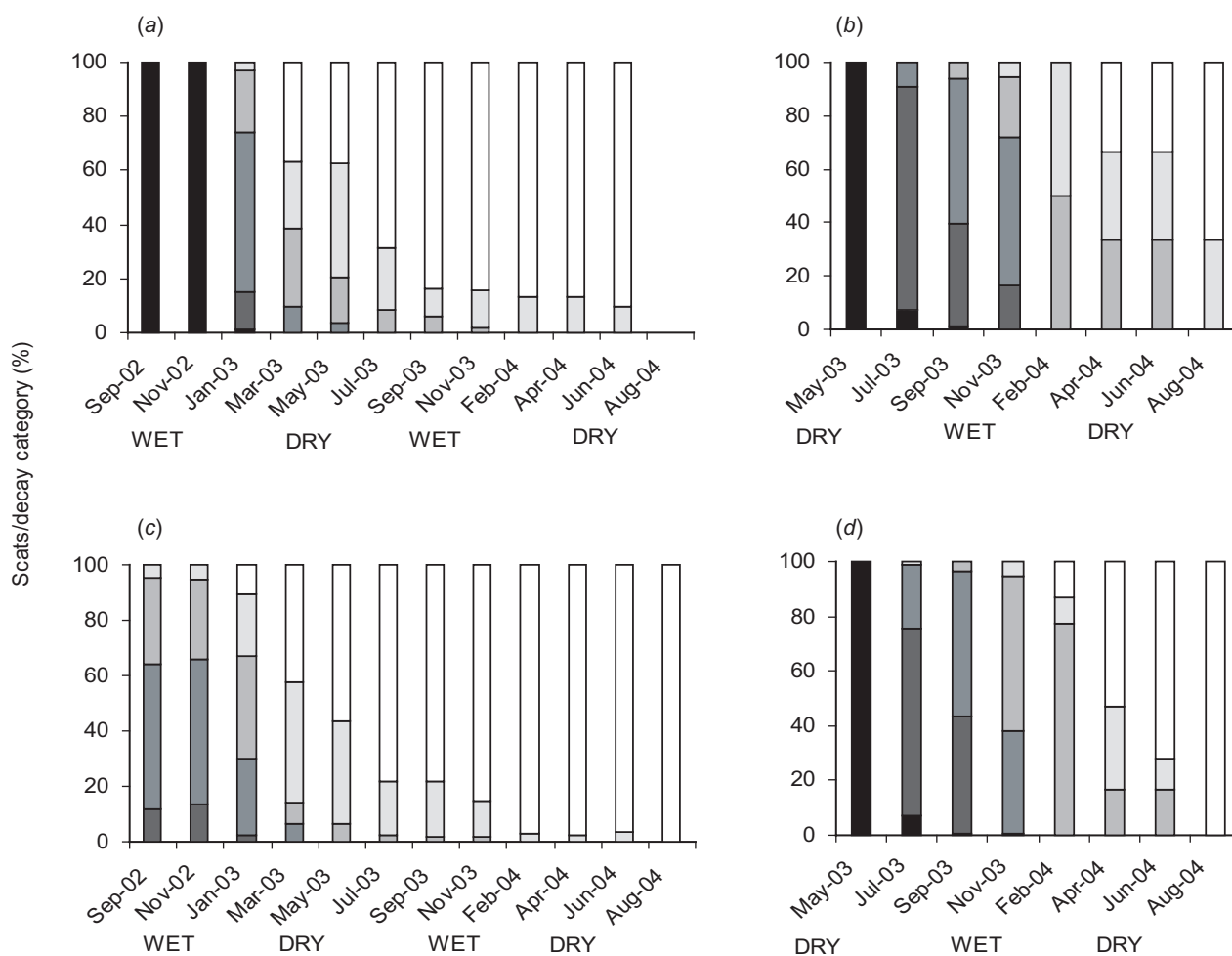


Fig. 5. Percentage of scats decaying to each category with time on (a) sandy litter substrate in Experiment A, (b) sandy litter substrate in Experiment B, (c) rocky substrate in Experiment A, and (d) rocky substrate in Experiment B. Black, Category 1 (new, black and glossy); dark grey, Category 2 (matte black, no cracking); mid-grey, Category 3 (black, cracking, 0–25% fawn fibres); light grey, Category 4 (black, 25–50% fawn fibres); very light grey, Category 5 (grey, 50–75% fawn fibres); white, Category 6 (grey, 75–100% fawn fibres).

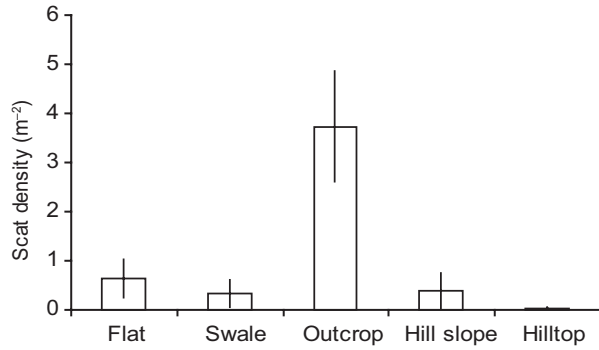


Fig. 6. Regression coefficients and 95% confidence intervals of scat density of *Petrogale brachyotis* as predicted by habitat in generalised least-squares modelling.

guished from those of other species, including the similarly sized, but more rufous-coloured and finer-textured, rock ringtail possum scats that are found in the same rocky habitats. Thus scats can be used successfully to determine the presence of *P. brachyotis* and to clarify the distribution of the species. Densities of *P. brachyotis* scats were highest in rocky habitats and they also persisted longer on rock than on sandy substrates. Therefore, surveys should target rocky habitats to most efficiently identify the presence of *P. brachyotis* in an area.

Basic measurements of size, shape and colour also enabled acceptably accurate identification of the scats of other macropod species in the region. Scats are inherently variable in appearance. So, to maximise accuracy of identifi-

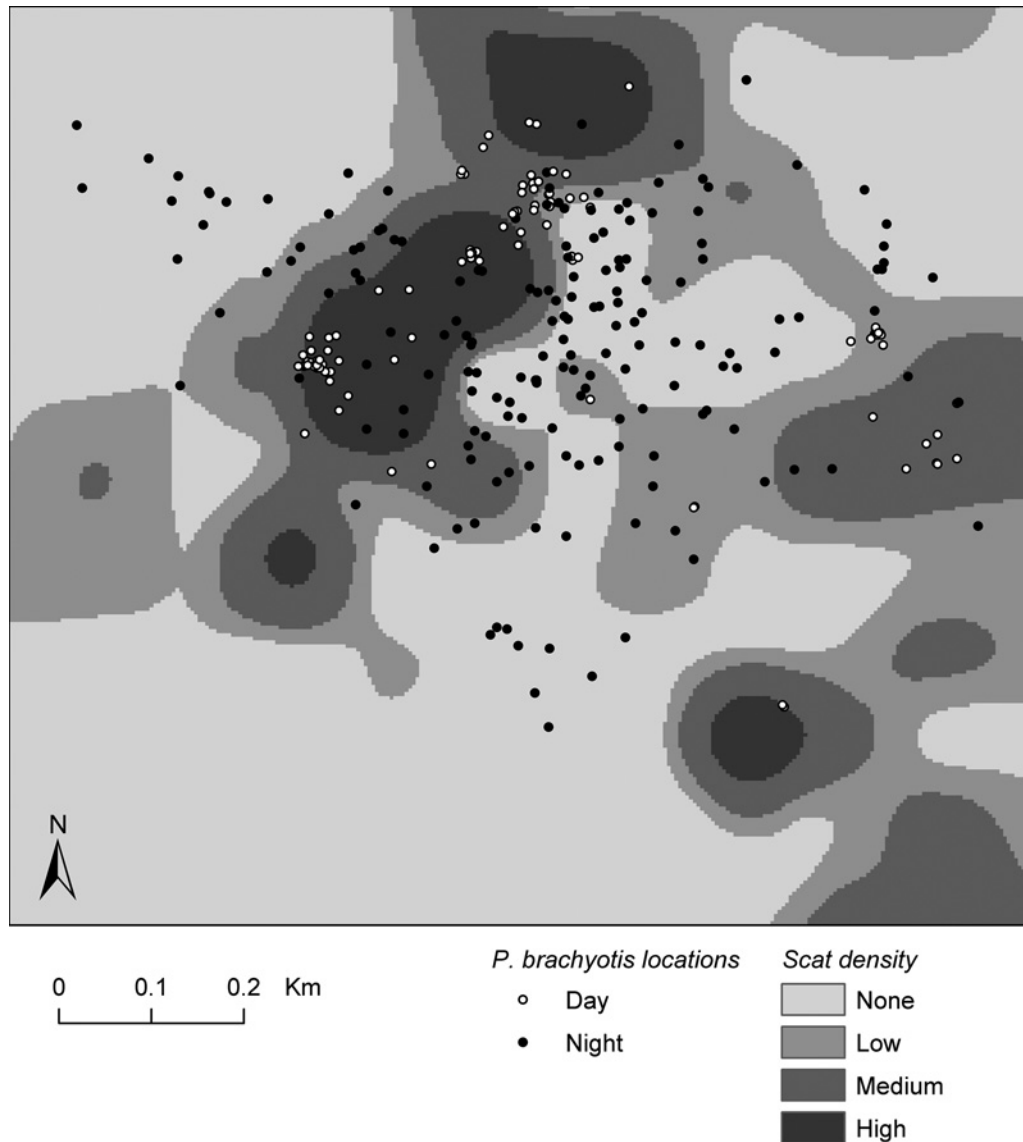


Fig. 7. Diurnal and nocturnal fixes of eight radio-tracked *Petrogale brachyotis* (Telfer and Griffiths 2006) over a regularised spline interpolation of scat densities at Litchfield National Park in July/August 2003.

caution, a large number of scats should always be measured and the habitats whence the scats were collected should also be known. For example, some scats of the black wallaroo (*M. bernardus*) and common wallaroo (*M. robustus*) overlap in size and shape and can be confused when based on basic observations. However, the scats of the two species can be reliably identified by measuring their width. Since scats of the juveniles of one species tend to overlap in size with the scats of adults of smaller, closely related species, it is the largest scats found that are most helpful for identification. For cryptic and largely nocturnal species, such as *M. bernardus* and *M. robustus*, scats offer a far greater probability of detection than do alternative techniques such as observation and trapping, and hence represent an important technique for studying these species.

Of the species examined, the scats of the nabarlek (*P. concinna*) are the most unsuitable for use in surveys of distribution. The scats of *P. concinna* can look the same as scats of young *P. brachyotis*, with whom they live sympatrically at many sites. Since positive visual identification of individuals of *P. concinna* continues to be problematic due to their physical similarity to *P. brachyotis*, the most effective method for identifying the presence of *P. concinna* would be analysis of the DNA in scats. This process is feasible for genetically distinct species such as these (M. Eldridge, personal communication), and is becoming more viable as these molecular techniques are refined (Davison *et al.* 2002; Piggott 2004).

Surveying habitat use

A major assumption of using scats to determine habitat use is that the rate of loss of scats is equal across habitats. We found that *P. brachyotis* scats persisted longer on rocky substrates than on sand with litter. Therefore, if defaecation rates are equal on these two substrates, more scats will be found in rocky areas. Yet this effect was strongly seasonal, with loss of scats being significantly different between habitats only in the wet season due to runoff and sometimes in the dry season due to fire. Thus, scats can be used to survey habitat use in the monsoon tropics, but surveys should be conducted in the early dry season before burning or in the late dry season after burning. Furthermore, since substrate also affected the rate of decay and apparent 'age' of scats, only new (dark and glossy) scats should be used in surveys of the relative use of habitats.

Our analysis of the distribution of *P. brachyotis* scats suggested that examining scat densities can be an effective method for determining broad habitat preference. Scat distribution ranked the use of habitats in the same order as found with radio-telemetry (Telfer and Griffiths 2006). Yet there were fine-scaled differences in the relative use of habitats determined by the two methods. For example, in our study the scat densities suggested that outcrops were used significantly more than other habitats, whereas the radio-tracking

fixes suggested that adjacent flat areas were used to a similar extent as the outcrops. This difference may result from a bias in scat density towards rocky areas due to either the lower disappearance rates of scats from rocky habitats or behavioural effects such as higher defaecation rates in rocky habitats immediately after animals have been resting. Alternatively, the use of the outcrops may have been under-represented by the weighting of diurnal to nocturnal fixes in the telemetry study (Telfer and Griffiths 2006).

While scat distribution can show broad habitat preferences, our results suggested that it was not a good surrogate for total area used by *P. brachyotis*. Radio-tracked animals ranged up to 480 m from their shelters (Telfer and Griffiths 2006), but at the site in this study and in transects measured at many sites across the landscape (Telfer 2006), scats of *P. brachyotis* were found only up to 200 m from potential rocky shelter sites. Other studies of rock-wallaby species also report absence of scats at distances between 50 and 200 m from diurnal shelters (Lunney *et al.* 1996; Jarman and Capararo 1997; Geelen 1999). However, it is well known that rock-wallabies commonly range to greater distances than this (Lim 1987; Horsup 1994). Jarman and Capararo (1997) argue that the probability of a rock-wallaby occurring at any point is dependent upon both the wallaby's preference for that habitat and the distance of that point from the wallaby's shelter sites. While we support this model of exponentially declining densities of scats with increasing distance from a diurnal shelter, our data suggest that the zone of wallaby activity actually continues well beyond the limit of scats that surround a point-source such as a den. We believe the failure to find scats >200 m from shelters is due to the lower scat densities caused by animal dispersion associated with radial foraging rather than because rock-wallabies rarely defaecate this far from shelters.

We are confident that scats can accurately show broad habitat use for other rock-dwelling macropods but may not be able to indicate fine-scale differences in the relative use of habitats or the extent of space used. Thus, such data are appropriate for addressing questions of which habitats are used and interspecific differences in habitat use, rather than the relative use of different habitats. For other macropod species that do not use permanent fixed shelters, the relative use of habitats and total space used may match more closely with the distribution of scats because these species are not 'tethered' to a particular location such as a den. In order to use scat densities to infer fine-scale, relative use of habitats, future research should determine the probability of finding scats in each habitat, data that can then be used to adjust the densities of found scats (as has been done for radio-location data collected with global positioning systems: Frair *et al.* 2004).

Monitoring of site occupancy

Scats provide wildlife managers with a simple and cost-effective method of monitoring populations of rock-dwelling macropods such as *P. brachyotis*. We suggest that permanent

plots or fixed search areas should be established in rocky habitats where existing scats are present to maximise the chance of detecting changes in the use of an area by the target species. Rocky sites should be selected because they are core areas of use, and dark and glossy scats, known to be only a few months old in these habitats, will signal recent use of an area of interest. In contrast, weathered grey scats can persist up to two years and are of variable age so are not useful for surveys of occupancy. Since scats are lost most rapidly in the wet season, monitoring at this time of year would give the most precise measurements of recent occupancy. However, the dry season will be the most successful time for monitoring because of the lower probability of detecting 'false absences' (MacKenzie *et al.* 2002).

Conclusion

Use of scats offers an efficient and cost-effective technique for studying elusive species such as the rock-dwelling macropods of the monsoon tropics. For accurate identification of scats of sympatric macropod species, large sample sizes should be examined and the habitats in which the scats are collected should be known. Studies of habitat use in the tropics should use new, dark glossy scats only and be conducted in the dry season. Scats can effectively indicate broad habitat use and show core areas of use of species such as *P. brachyotis*, but may not show the total area used.

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