



Does aridity affect spatial ecology? Scaling of home range size in small carnivorous marsupials

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Abstract

The aim of our study was to determine how body mass affects home range size in carnivorous marsupials (dasyurids) and whether those species living in desert environments require relatively larger areas than their mesic counterparts. The movement patterns of two sympatric species of desert dasyurids (body mass 16 and 105 g) were investigated via radio-telemetry in southwestern Queensland and compared with published records for other Australian dasyurids. Both species monitored occupied stable home ranges. For all dasyurids, home range size scaled with body mass with a coefficient of > 1.2 , almost twice that for metabolic rate. Generally, males occupied larger home ranges than females, even after accounting for the size dimorphism common in dasyurids. Of the three environmental variables tested, primary productivity and habitat, a categorical variable based on the 500 mm rainfall isopleth, further improved model performance demonstrating that arid species generally occupy larger home ranges. Similar patterns were still present in the dataset after correcting for phylogeny. Consequently, the trend towards relatively larger home ranges with decreasing habitat productivity can be attributed to environmental factors and was not a result of taxonomic affiliation. We therefore conclude that alternative avenues to reduce energy requirements on an individual and population level (i.e. torpor, basking and population density) do not fully compensate for the low resource availability of deserts demanding an increase in home range size.

Keywords Arid versus mesic · Energy turnover · Locomotion · Torpor

Introduction

Familiarity with habitat and surroundings is of utmost importance for optimal foraging, predator avoidance and reproduction. Hence, the movement of most animals is spatially restricted and the area that encompasses these movements is referred to as an animal's home range (Burt 1943). As home range size varies vastly amongst species, trends and patterns are discernible even in datasets with variable sampling regimes and by geometrical rather than statistical home range models such as Minimum Convex Polygon (MCP) (Lindstedt

et al. 1986; McNab 1963; Ottaviani et al. 2006). One important factor that determines the size of a home range appears to be the resource requirements of an animal and therefore home range size increases with body size (Harestad and Bunnell 1979; Lindstedt et al. 1986; McNab 1963).

Usually, resource availability is not uniform but is affected by the diet of an animal and by the heterogeneity in the environment. As animal prey occurs generally at lower densities than plants, carnivores tend to occupy larger home ranges than similar-sized herbivores (Harestad and Bunnell 1979; Kelt and Van Vuren 2001; Lindstedt et al. 1986; Ottaviani et al. 2006). Furthermore, home range size should be inversely related to habitat productivity. This assumption is supported by latitudinal data on the home range size of North American carnivores. At higher latitudes, the home ranges of large carnivores are about twice as large as those of the same species further south (Gompper and Gittleman 1991; Lindstedt et al. 1986) presumably because of lower prey availability and perhaps also increased thermoregulatory costs. Similarly, in Australian macropods, medium to large marsupials, home range size is predominantly influenced by annual rainfall

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and hence increases with the aridity of the habitat (Fisher and Owens 2000). However, as both of these examples comprise medium- to large-sized mammals, it remains unresolved whether this scenario can be generalised and whether it is applicable also to smaller mammals especially since it has been proposed that home range size does not shrink below a minimum for mammals with a body mass (BM) below 100 g (Kelt and Van Vuren 2001).

The mass-specific cost of transport in medium-sized and larger species is comparatively low (Schmidt-Nielsen 1972). Therefore, an enlarged home range to compensate for low food densities can be achieved without a disproportional increase in energy expenditure. In contrast, in small terrestrial species, the scope for long-distance movements is much more limited by transport costs (Schmidt-Nielsen 1972; Tucker 1970), which ultimately should curb home range size. Alternatively, a slump in resource availability often results in lower population densities, and animals can also curb resource demands via food hoarding and also by lowering their metabolic rate. Despite such potential energy-saving mechanisms, species living in areas with extremely low and patchy food availability such as deserts might have to move continuously from one suitable habitat patch to another (i.e. no discernible home range at least in the longer term). For example, some, but certainly not all, of the small mammal species inhabiting the vast arid zones of Australia appear to either regularly shift their home ranges or show “vagrant” behaviour (Dickman et al. 1995; Morton 1978a; Read 1984). Indeed, movements of marked individuals between trapping grids over many kilometres (Dickman et al. 1995; Letnic 2002) have been documented, which might assist them with exploiting temporarily and spatially limited, favourable conditions following rain (Dickman et al. 1995; Masters 1993).

Here, we present original data for two different-sized species of dasyurid marsupials measured at the same time and location. Dasyurids are a family of small to medium-sized marsupials that can be found in all of Australia’s habitat types and have a relatively uniform insectivorous/carnivorous diet (Dickman 2003; Hume 2003). In this respect, dasyurids match paccental insectivores and carnivores, but the lifespan of dasyurids is unusually short with some species showing a total male die off after mating at 11 months and even the larger species rarely living longer than 5 years (Tyndale-Biscoe 2005). To interpret our data for the two arid zone species in a meaningful ecological context, we sourced all comparable data for this group of marsupials from the literature. With this increased dataset, we were able to test three hypotheses concerning the spatial behaviour of small mammals. Firstly, we predicted that home range shifts are rare events and that most species living in resource-poor habitats are able to establish at least temporarily stable home ranges (i.e. home ranges might shift over time, but animals are not vagrant). Secondly, we expected that home range size scales with BM but given

that Australia after Antarctica is the most arid continent, we predicted some differences to the scaling found in placental mammals with a similar insectivorous/carnivorous diet from more productive habitats in the northern hemisphere (Kelt and Van Vuren 2001). Thirdly, we expected that habitat productivity affects home range size and therefore home range size should be proportionally larger in arid species compared to their mesic counterparts. We also expected that the extensive use of torpor by dasyurids especially in arid sites could compensate for changes in resource availability to some degree.

Methods

Home range size and movement patterns of two sympatric species of arid zone dasyurids were investigated using radio-telemetry, which, if conducted over prolonged periods, is known to provide a more reliable estimate of home range area than trapping (Pavey et al. 2003). Stripe-faced dunnarts (*Sminthopsis macroura*, 6 males, 2 females) and kowaris (*Dasyuroides byrnei*, 4 males, 2 females) were radio-tracked at Astrebla Downs National Park, southwestern Queensland (24°10’S, 140°34’E) during June–August 2007. Two ~1-month periods of fieldwork were conducted, separated by a return trip to the University of New England for equipment repairs and restocking. The park is characterised by plains of deep cracking clay soils interspersed with gibber (ironstone pebbles). Following rare rainfall events, ephemeral Mitchell grass (*Astrebla* spp.) covers the plains. During the usual dry periods, however, aboveground vegetation can be found only along some of the widely spaced dry riverbeds. The study was conducted during such a dry period.

Dunnarts were trapped in pitfall traps (60 cm deep, 15 cm diameter storm-water pipes) linked with a drift fence while the larger kowaris were captured in box aluminium traps (33 × 9 × 9 cm; Type A; Elliott Scientific Equipment, Upwey, Australia) (Körtner and Geiser 2011).

To prevent animals shedding transmitters and in order to minimize external obstructions that could interfere with movement, transmitters (Sirtrack, Havelock, New Zealand) were implanted intraperitoneally under general oxygen/isoflurane anaesthesia (for details see Körtner and Geiser 2009). For dunnarts, the transmitter mass was close 10% of BM, whereas for kowaris, it was substantially less (~3%). Implanted transmitters in this mass range do not affect the locomotor performance of small dasyurids (Rojas et al. 2010) and given the high mass-specific normothermic metabolic rate are also unlikely to increase energy demands in the longer term. Animals were tracked daily to their rest site, and the location was determined using a handheld GPS (Garmin, 12x, Oregon, USA). Individual burrows were then marked with flagging tape. In addition, we were able to supplement nest site data with nighttime records for one kowari; most of the other individuals tried

to evade an approaching person when active at night and therefore tracking during the activity period was limited to the few occasions when an animal remained stationary during the radio-tracking process. With the exception of the period when females nurse young in a nest, most dasyurids move between dens on an almost daily basis and although the inclusion of activity locations does increase home range estimate to a degree, perhaps partly because of triangulation errors, rest-phase locations appear to provide a more than reasonable estimate (Glen and Dickman 2006). As no triangulation had to be employed, the spatial error would have been that of the handheld GPS and therefore in the order of 1–10 m.

The existence of a temporal stable home range as opposed to random movement between sequential locations was assessed with the “Site Fidelity Test” of the software package Animal Movement V2 (Hooge and Eichenlaub 1997). In this test, 50 MCPs (minimum convex polygons) were calculated based on the original distance between sequential locations, but randomized direction and compared with the original MCP for the tested individual (see below). Home range size was calculated as MCP (Animal Movement V2; Hooge and Eichenlaub 1997) to allow comparisons with literature data. The uniformity of the landscape at the study site and the even scattering of location records facilitated this geometrical method. In addition, Kernel home range (90% and 50 isopleths) was calculated with the same software package using the default settings for an ad hoc calculation of a smoothing parameter (Hooge and Eichenlaub 1997). The effect of sample size on MCPs was assessed by plotting home range size against number of location records, using stepwise removal of a random number of records from each animal’s dataset. Data were processed with the “MCP Sample size Bootstrap” procedure in Animal Movement V2 (Hooge and Eichenlaub 1997). Curves for our data tended to reach an asymptote at about 20–30 location records.

Overlap between home ranges of two neighbouring individuals was analysed by intersecting the two home-range polygons (100% MCP) and calculating percentage overlap. Because this percentage is a function of home range size and therefore generally differs between the two members of the pair analysed, the following index was used including the home range size of both individuals (Körtner et al. 2007):

$$\left[\left(\text{area}_{\alpha\beta} / \text{home range}_{\alpha} \right) * \left(\text{area}_{\alpha\beta} / \text{home range}_{\beta} \right) \right]^{0.5}$$

where $\text{area}_{\alpha\beta}$ is the overlapping area and $\text{home range}_{\alpha}$ and $\text{home range}_{\beta}$ are the home ranges of individual α and β , respectively.

Selection of published data

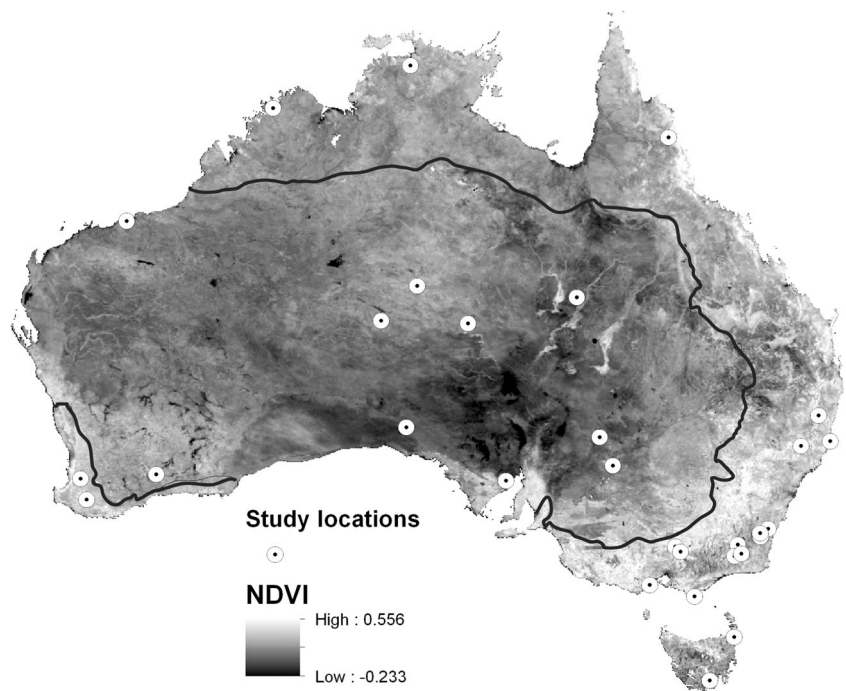
The dataset used for our analyses to assess the influence of BM, sex, habitat type, rainfall and primary productivity on

home range size comprised original records for two sympatric arid zone species in addition to those on 17 species derived from existing literature (Table 2).

Our order-wide analysis had to be restricted to the geometric 100% MCP estimate to maximize the number of species available for testing. To avoid methodological bias, all home range size estimates had to be based on radio-telemetry of free-ranging animals in their natural habitat. However, like all monitoring methods, fitting radio-transmitters to animals will have some impact on animals and a potential but unknown bias associated with the transmitter design, body size and ecology has to be expected. In one publication on *Antechinus stuartii*, numeric MCP values were not given and home range size was obtained from Fig. 4 in Lazenby-Cohen and Cockburn (1991). Where BM data were not presented in the original publication, we substituted these from other published records, preferably from the same study population (Table 2). If not included in the original publication, data on average, yearly rainfall was extracted from maps for rainfall isopleth provided by the Australian Bureau of Meteorology (BOM). To describe primary productivity of the various study locations, a normalized difference vegetation index (NDVI), regularly used in ecological studies (Pettorelli et al. 2011), was employed. The NDVIs were sourced from half-yearly satellite images showing an infrared index (IF) representing vegetation cover, available from BOM for the years 1992–2010. A higher value indicates a more productive environment. This time frame covered most, especially the arid zone studies, and for studies conducted earlier or later, the closest yearly average (i.e. two images) was used. Log-transformed home range data were analysed using a linear mixed effects model (R-package “nlme”, “lme4”) with species as a random factor to account for the multiple data points available for some species (Table 2). All models included “log-transformed BM” as well as “sex” and either the factor “habitat” (e.g. mesic versus arid) or the continuous variables “rainfall” (yearly average) and “NDVI”. For habitat, a rainfall threshold of 500 mm per year was chosen separating forested habitats from semiarid/arid grass- and shrub-land (Fig. 1). To facilitate meaningful biological interpretation of models, only models limited to first-order interaction terms were considered. Subsequent model simplification and selection was based on the Akaike’s Information Criterion (AIC) and Akaike weights (w_i), but P value selection would have achieved a similar solution. A conditional R^2 for the mixed-effects models was calculated with the R-package “MuMIn”. Considering the small sample size for female stripe-faced dunnarts and female kowaris (see below), we repeated the analyses after removing the two data points.

To account for phylogenetic affiliation, we used the “pglS” function in the R-package “caper” based on the phylogenetic tree given by Bininda-Emonds et al. (2008) and created in the R-package “ape”. Such a correction can include only one data

Fig. 1 Australian map showing the study locations. The underlying grey-scale image represents an infrared index for NDVI for the time period May to October 2000, as an example. The 500-mm rainfall isopleth is also shown as a black line with the interior receiving less rain



point per species and does not accept a zero distance value for populations of one species. Therefore, if multiple data points were available per species, these were averaged. We made one exception for the two datasets for *Dasyurus geoffroii*, as they came from a mesic and an arid site, and a very small distance value for the two populations was created. Given the strong sexual dimorphism for body and home range size in dasyurids, neither solution can be applied to combine male and female values. Consequently, male and female data values were not averaged and the tests were run twice, for males and females separately. The `pgls` function incorporates a covariance matrix based on the branch length of the taxonomic tree to account for the non-independence of the data points and also allows the inclusion of all the environmental variables mentioned above, and model selection was again based on AIC. To facilitate model comparison using AIC, branch length transformation remained constant at the default setting with *lambda*, *delta* and *kappa* fixed to “1” assuming a Brownian model of evolution.

Significance was assumed at a 5% level. Data are presented as the mean \pm 1SD.

Results

Sminthopsis macroura

Stripe-faced dunnarts (BM = 16.9 ± 1.3 g, $n = 8$) were tracked for an average of 26.6 ± 13.8 days (Table 1). Dunnarts always sheltered in soil cracks, some of which were used for several consecutive days or were later re-visited. A temporarily stable home range was statistically confirmed ($P < 0.02$, i.e. less than

2% of the MCPs calculated by randomising movement directions were smaller than the real MCP for an individual) for six of the eight dunnarts. The two individuals for which the test was non-significant were those with the smallest home ranges. Male and female dunnarts occupied similar-sized relatively small areas (males 0.68 ± 0.66 ha; females 0.63 ± 0.75 ha; $T_1 = 0.09$, $P = 0.94$). However, MCP home range size ranged from 0.05 to 1.7 ha (Table 1) and the sample size, especially for females, might have been too low to detect sex-specific differences. Animals stayed within this home range throughout two consecutive 1-month survey periods and could be located every day. Home ranges of the monitored animals did not overlap.

Dasyuroides byrnei

Kowaris (BM = 113.9 ± 12.4 g, $n = 6$) were radio-tracked for an average of 23.2 ± 5.8 days (Table 1). All animals were tracked to the end of our two surveys except for one animal for which transmitter failure was confirmed by re-capture. Kowaris were too large to enter most soil cracks and nested predominantly in burrows constructed by the bilby (*Macrotis lagotis*, BM = ~ 2 kg), occasionally in smaller burrows presumably excavated by long-haired rats (*Rattus villosissimus*, BM = ~ 130 g) and in some of the larger cavities formed by drying clay. Kowaris re-visited burrows often, and site fidelity was statistically confirmed ($P < 0.05$) for five of the six individuals. The home range size of the four males was on average 68.7 ± 70.8 ha. In addition, radio-tracking of one female (no. 3, Table 1) yielded sufficient different locations to warrant a home range estimate 16.5 ha, smaller than for any of the

Table 1 Individual records of desert dasyurids measured at Astrebla Downs National Park for this study. Id stands for individual, BM for body mass and MCP for minimum convex polygon

| Species | Id | Sex | BM (g) | No. of records | MCP (ha) | Kernel 90% | Kernel 50% |
|-----------------------------|------|-----|--------|----------------|-------------------|------------|------------|
| <i>Sminthopsis macroura</i> | Sm01 | M | 15.0 | 25 | 0.50 | 1.74 | 0.30 |
| | Sm02 | M | 17.5 | 15 | 0.05 | 0.07 | 0.01 |
| | Sm03 | M | 18.3 | 23 | 1.31 | 0.84 | 0.15 |
| | Sm04 | F | 15.7 | 58 | 1.16 | 0.65 | 0.09 |
| | Sm05 | M | 18.3 | 29 | 1.70 | 1.27 | 0.23 |
| | Sm06 | M | 15.3 | 27 | 0.25 | 0.34 | 0.09 |
| | Sm07 | F | 17.4 | 24 | 0.10 | 0.46 | 0.10 |
| | Sm08 | M | 17.3 | 24 | 0.29 | 0.53 | 0.13 |
| <i>Dasyuroides byrnei</i> | Db01 | M | 111.8 | 20 | 26.05 | 36.83 | 8.93 |
| | Db02 | M | 118.6 | 23 | 36.11 | 53.85 | 6.47 |
| | Db03 | F | 102.6 | 34 | 16.54 | 9.69 | 2.68 |
| | Db04 | M | 134.5 | 27 | 174.64 | 123.87 | 17.98 |
| | Db05 | M | 115.7 | 31 | 38.15 | 26.63 | 4.2 |
| | Db06 | F | 100.4 | 23 | 0.65 ^a | | |

^a Value excluded from analysis, see text

males. The second female (no. 6), the last animal implanted, resided in the same burrow for the entire 23 days of the tracking (data for this individual were excluded from further analysis as not enough different location records could be obtained). Three of the males and the two females were trapped in the same area, and all their home ranges overlapped by an average of $21.6 \pm 16.5\%$ between pairs. Furthermore, kowaris shared burrows extensively. During the entire tracking period for female no. 6, this female shared the same burrow with female no. 3, which by then had also stopped moving between burrows at a time when females carried pouch young (Körtner and Geiser 2011). Therefore, the estimate of the home range area for this species excludes the time of lactation during which home range size is presumably temporarily reduced in females and not measurable with our method.

Interspecies and sex comparisons

Including the species studied here, we were able to obtain home range estimates based on radio-telemetry of 18 species of dasyurid marsupials (Table 2). Similar to our data, for the majority of these studies, radio-tracking was restricted or at least focused on rest-time locations. For most studies, the dataset is quite small reflecting the effort of radio-tracking wild animals (Table 2). Nevertheless, the dataset represents the entire BM range of dasyurids found in Australia, ranging from 7 to 9000 g. However, larger dasyurids are absent or extinct in arid environments with the exception of a few surviving small populations of the western quoll (*Dasyurus geoffroii*, BM 900-1300 g); fortunately, one publication on home range size for this species was available (Rayner et al. 2012). Overall, the home range size of dasyurids scaled with BM with a scaling

coefficient of 1.27 ± 0.13 ($P < 0.001$, $R^2_c = 0.93$; Table 3; Fig. 2).

Amongst dasyurids, males were on average larger than females (Paired t-test: $t_{22} = 3.54$, $P = 0.002$). However, the BM effect alone did not account for the differences in home range size and including sex into subsequent models improved the AIC (Table 3).

Of the environmental variables, the inclusion of rainfall did not improve the model, but both habitat and NDVI did (Table 3). As far as habitat productivity is concerned, the average NDVI index was 0.157 for the arid species and 0.386 for their mesic counterparts. The most parsimonious model included a combination of both variables and a number of interaction terms between them (Tables 3 and 4). Removing the female data for kowaris and stripe-faced dunnarts (low sample size) yielded the same result with AIC values that differed by less than 1 for all models tested. Therefore, based on AIC selection as well as on significance criteria, habitat productivity appears to affect home range size in both sexes of dasyurids (Fig. 3). However, this conclusion requires confirmation that phylogeny does not account for the observed patterns.

Phylogenetically corrected data again showed an increase of home range size with BM; importantly, models improved with the inclusion of environmental variables. In contrast, to the uncorrected data, the most parsimonious models for both sexes included only Habitat and not NDVI (Table 5) with the model parameter for the most parsimonious models listed in Table 6. For both sexes, models including interaction terms were almost identical in their performance as those that excluded them (i.e. $\Delta AIC < 2$). As the structure of the most parsimonious models differed from the one for the uncorrected data,

Table 2 Body mass (BM) and home range size (minimum convex polygon, MCP) of 18 species of dasyurid marsupials plus details of the study sites. NPVI is the normalized difference vegetation index. The number in brackets after the species name refers to the number of individuals recorded

| Species | Latitude | Longitude | Habitat | Rain fall | NDVI | BM male | MCP male | BM female | MCP female | Reference |
|--|----------|-----------|---------|-----------|-------|---------|----------|-----------|------------|---|
| Reference | | | | mm/y | IF | g | ha | g | ha | |
| <i>Sminthopsis macroura</i> (8) | -24.1667 | 140.5667 | Arid | 250 | 0.073 | 16.6 | 0.68 | 16.6 | 0.90 | Present study |
| <i>Dasyuroides byrnei</i> (5) | -24.1667 | 140.5667 | Arid | 250 | 0.073 | 117.6 | 68.74 | 93.2 | 16.5 | Present study |
| <i>Planigale gilesi</i> (3) | -32.5000 | 142.3333 | Arid | 240 | 0.153 | 6.8 | 0.12 | NA | NA | Warnecke et al. (2012) |
| <i>Sminthopsis crassicaudata</i> (6) | -32.5000 | 142.3333 | Arid | 240 | 0.153 | 12.2 | 1.60 | NA | NA | Warnecke et al. (2012) |
| <i>Sminthopsis macroura</i> (2) | -31.0833 | 141.6833 | Arid | 233 | 0.084 | 16.3 | 5.20 | NA | NA | Warnecke et al. (2012) |
| <i>Sminthopsis leucopus</i> (12) | -38.3830 | 144.1333 | Mesic | 900 | 0.359 | 24.0 | 1.22 | 24 | 0.98 | (Laidlaw et al. (1996) |
| <i>Sminthopsis psammophilia</i> (16) | -31.9170 | 134.6650 | Arid | 450 | 0.180 | 35.7 | 14.1 | 30.8 | 10.7 | Churchill (2001) |
| <i>Dasykaluta rosamondae</i> (11) | -20.4000 | 118.5333 | Arid | 314 | 0.189 | 27.1 | 3.08 | 28.2 | 0.98 | Körtner et al. (2010) |
| <i>Pseudantechinus macdonnellensis</i> (6) | -23.6166 | 132.7500 | Arid | 321 | 0.229 | 32.1 | 0.98 | 28.3 | 0.31 | Pavey et al. (2003) ^a |
| <i>Antechinus stuartii</i> (10) | -35.6166 | 149.9166 | Mesic | 800 | 0.451 | 22.5 | 3.2 | 22.5 | 1.7 | Lazenby-Cohen and Cockburn (1991) |
| <i>Antechinus swainsonii</i> (7) | -36.4000 | 148.4333 | Mesic | 1765 | 0.374 | 65.0 | 0.56 | 41 | 0.33 | (Sanecki et al. (2006) |
| <i>Antechinus minimus</i> (6) | -38.9500 | 146.3166 | Mesic | 1054 | 0.463 | 65.0 | 2.35 | 42 | 1.15 | Sale and Arnould (2009) |
| <i>Dasyercus blythi</i> (8) | -25.3333 | 131.0033 | Arid | 295 | 0.176 | 85.0 | 25.5 | 57.4 | 10.8 | Körtner et al. (2007) |
| <i>Dasyercus blythi</i> (8) | -25.4667 | 135.2500 | Arid | 150 | 0.129 | 83.4 | 26.3 | 62 | 24.1 | Körtner et al. (2016) |
| <i>Phascogale tapoatafa</i> (40) | -36.4833 | 145.3889 | Mesic | 600 | 0.434 | 230 | 106.2 | 155 | 41.2 | Soderquist (1995) |
| <i>Phascogale tapoatafa</i> (9) | -36.7500 | 145.6290 | Mesic | 600 | 0.380 | 248.5 | NA | 136 | 5.58 | van der Ree et al. (2001) |
| <i>Phascogale tapoatafa</i> (11) | -34.1666 | 116.5833 | Mesic | 600 | 0.464 | NA | NA | 123.6 | 15.5 | Rhind and Bradley (2002) |
| <i>Dasyurus hallucatus</i> (15) | -12.7167 | 132.4167 | Mesic | 1200 | 0.359 | 760 | 99 | 460 | 35.0 | Oakwood (2002) |
| <i>Dasyurus hallucatus</i> (22) | -14.8167 | 125.7167 | Mesic | 1548 | 0.255 | 577.2 | 74.8 | 386.7 | 11.6 | Cook (2010) |
| <i>Dasyurus viverrinus</i> (38) | -43.1000 | 147.0700 | Mesic | 1250 | 0.417 | 1387 | 50.9 | 862 | 34.7 | Godsell (1983) |
| <i>Dasyurus geoffroii</i> (9) | -33.1417 | 116.2983 | Mesic | 1233 | 0.364 | 1309 | 415 | 891 | 90 | Serena and Soderquist (1989) ^b |
| <i>Dasyurus geoffroii</i> (6) | -32.5600 | 119.8300 | Arid | 340 | 0.288 | 1309 | 2125 | 891 | 189 | Rayner et al. (2012) ^b |
| <i>Dasyurus maculatus</i> (19) | -36.2579 | 149.1227 | Mesic | 800 | 0.521 | 2810 | 1755 | 1730 | 496 | Belcher and Darrant (2004) |
| <i>Dasyurus maculatus</i> (14) | -36.8350 | 148.6160 | Mesic | 600 | 0.432 | 2614 | 992 | 1621 | 244 | Claridge et al. (2005) |
| <i>Dasyurus maculatus</i> (8) | -30.0007 | 152.3833 | Mesic | 1250 | 0.560 | 3004 | 363 | 1680 | 133 | Glen and Dickman (2006) ^c |
| <i>Dasyurus maculatus</i> (10) | -31.2833 | 152.9500 | Mesic | 1546 | 0.437 | 3067 | 2908 | 2066 | 862.0 | Andrews (2005) |
| <i>Dasyurus m. gracilis</i> (6) | -16.2611 | 145.04166 | Mesic | 2500 | 0.445 | 1624 | NA | 1115 | 150.0 | Burnett (2001) |
| <i>Sarcophilus harrisii</i> (9) | -40.954 | 148.259 | Mesic | 800 | 0.349 | 9000 | 700.0 | 7000 | 1030 | Pemberton (1990) |

Where body mass was not listed in the original publication, it was substituted from references a–c

^a Geiser et al. (2002) these data are for the same individuals

^b Serena and Soderquist (1988) data for the same population

^c Körtner et al. (2004) average for the New England Tablelands where this study was conducted

they are not comparable. However, a tentative comparison of the models including only “BMlog” and Habitat and Sex without interaction terms for the uncorrected data could be made. In this case, the slope for BMlog (uncorrected: 1.38 ± 0.13 ; males corrected: 1.40 ± 0.24 ; females corrected: 1.45 ± 0.19) and habitat arid versus mesic (uncorrected -0.51 ± 0.19 ; males corrected -0.77 ± 0.21 ; females corrected -0.40 ± 0.15) were similar.

Discussion

The two sympatric species of desert dasyurids examined here showed movement patterns that were consistent with an at least temporarily stable home range, supporting our first hypothesis. Given that the available data span the whole body mass range of dasyurids and include species from all habitats, spatially restricted movement consistent with at least

Table 3 Model selection for original data without phylogenetic correction. Only the six most relevant models are shown

| Model | AIC | ΔAIC | w_i | R ² c |
|--|-------|-------|---------|------------------|
| 1 BMlog + sex + rainfall | 80.14 | 24.35 | 0.0005 | 0.93 |
| 2 BMlog | 70.11 | 14.32 | 0.0737 | 0.93 |
| 3 BMlog + sex | 66.69 | 10.9 | 0.4077 | 0.94 |
| 4 BMlog + sex + habitat | 63.09 | 7.3 | 2.4665 | 0.94 |
| 5 BMlog + sex + NDVI + BMlog:NDVI | 63.36 | 7.57 | 2.1550 | 0.94 |
| 6 BMlog + sex + NDVI + habitat + BMlog:NDVI + habitat:NDVI | 55.79 | 0 | 94.8966 | 0.94 |

temporarily stable home range appears to be widespread amongst mesic as well as desert dasyurids and true vagrancy is probably less common than had been previously assumed (Körtner et al. 2007; Masters 2003; Pavey et al. 2003). Nevertheless, radio-tracking studies did not and cannot cover the whole lifespan of an individual and therefore do not rule out temporary or permanent shifts in home range and long-distance movements, both of which evidently do occur (Dickman et al. 1995; Letnic 2002; Read 1984; Woolley 2017). Furthermore, if such events occur, they can easily result in a failure to re-locate a tagged animal. Nevertheless, successful radio-tracking within a restricted range appears to be the norm for studies on dasyurids suggesting that long-distance movements are rare and perhaps triggered by specific weather events (Dickman et al. 1995).

Since all the studied dasyurid marsupials (Table 2) occupy at least temporarily stable home ranges, the relationship between area requirements and their biology could be analysed. The home range of kowaris (~ 110 g) was substantially larger than

that of the simultaneously measured dunnarts (~ 17 g). Overall, in all dasyurids, home range size clearly scales with BM. Hence, this relationship that also has been found in other vertebrate groups (Kelt and Van Vuren 2001; Ottaviani et al. 2006; Perry and Garland 2002 and references within) applies to species of small marsupials too, supporting our second hypothesis. The sexual dimorphism in body size however does not fully explain the larger home range size of males of the generally polygamous dasyurids (Tyndale-Biscoe 2005); males are known to enlarge their home range at least temporarily to gain access to more than one female (Bos and Carthew 2008; Claridge et al. 2005; Godsell 1983; Körtner et al. 2004; Morton 1978a; Oakwood 2002; Pavey et al. 2003; Serena and Soderquist 1989; Soderquist 1995; Warnecke et al. 2012).

The general relationship between home range size and BM in dasyurids, with a scaling coefficient of 1.27 ± 0.13 , is similar to that of 1.23 ± 0.09 for placental mammals with a comparable carnivorous/insectivorous diet (Kelt and Van Vuren 2001). The slightly higher intercept for dasyurids might relate to the pronounced difference in the BM range between the two studies (Fig. 2) and/or to overall higher level of aridity found in Australia.

To explain this relationship, the log-linear relationship between energy expenditure and BM (Schmidt-Nielsen 1972) is commonly evoked (Lindstedt et al. 1986; Mace and Harvey 1983; McNab 1963), although the scaling coefficient for home range size found in the present and other studies (Kelt and Van Vuren 2001; Lindstedt et al. 1986; Ottaviani et al. 2006) is usually significantly larger (up to twofold) than those found for basal and also field metabolic rates (Nagy et al. 1999; Riek 2008; White and Seymour 2003). It has therefore been proposed that, within the same habitat, the density of

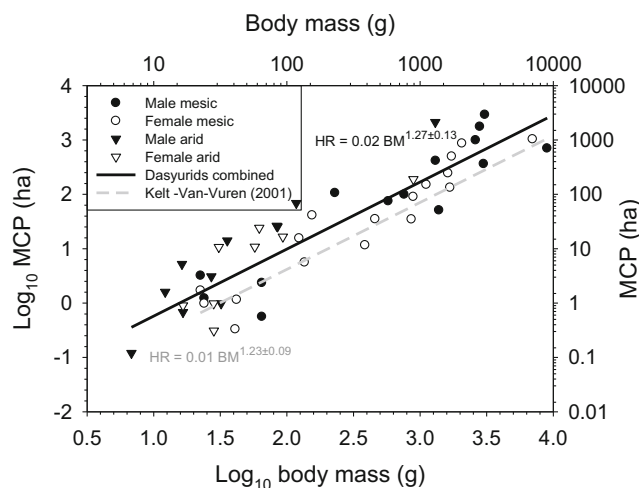
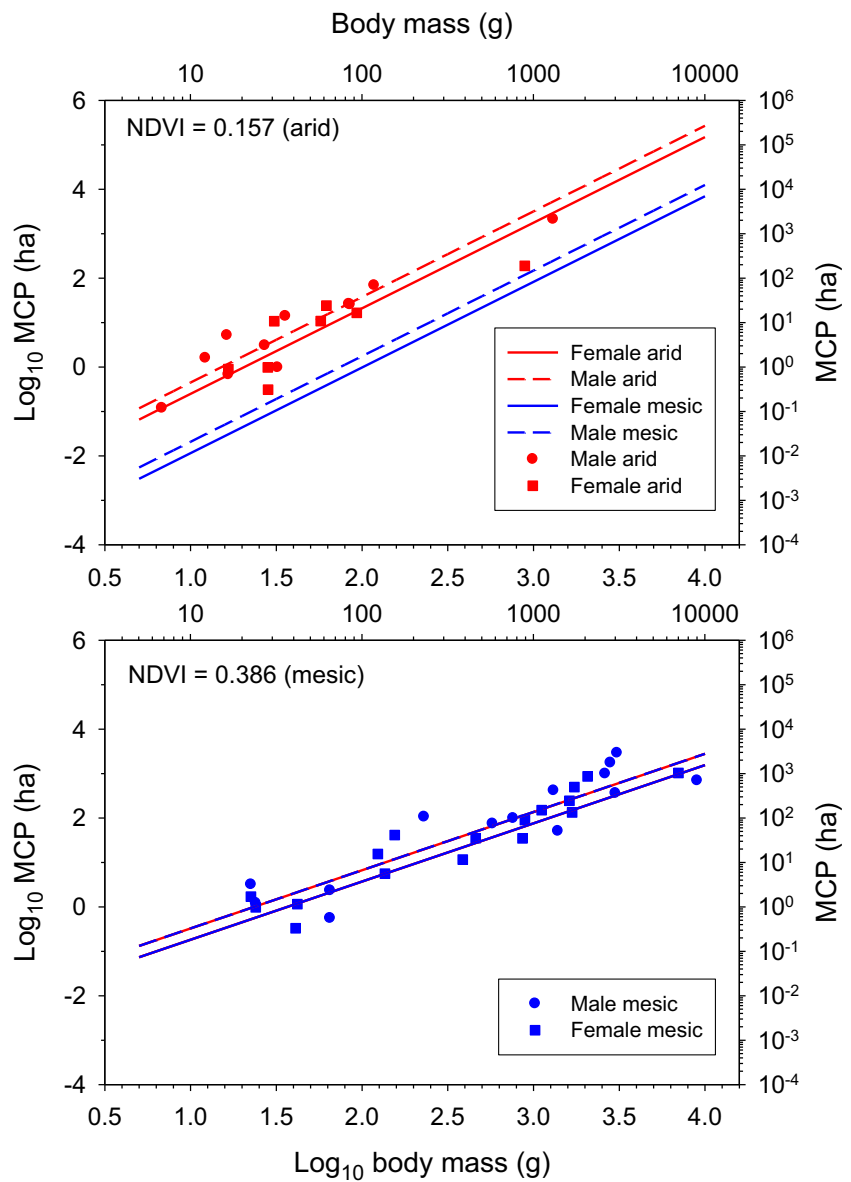


Fig. 2 Log-transformed home range size (minimum convex polygon in hectares) plotted against log-transformed body mass (g). The overall regression (mixed effects model with species as a random factor) was $\log_{10}(\text{home range}) = -1.607 (\pm 0.287) + 1.271 (\pm 0.130) \log_{10}(\text{body mass})$ and represents model 2 in Table 3. The solid line represents the regression through the whole dataset for dasyurid marsupials. For comparison, the dashed line illustrates the relationship for placentals with a similar insectivorous/carnivorous diet (Kelt and Van Vuren 2001). In this case, the dataset started at a body mass of approximately 22 g

Table 4 Model parameters for the most parsimonious model listed in Table 3

| Parameter | Value | SE |
|--------------|---------------|-------|
| Intercept | -2.862 | 0.638 |
| BMlog | 2.349 | 0.408 |
| Habitat | -2.244*arid | 0.884 |
| Sex | 0.254*females | 0.080 |
| NDVI | 2.100 | 2.139 |
| BMlog:NDVI | -2.688 | 1.091 |
| Habitat:NDVI | 5.813*arid | 2.949 |

Fig. 3 Illustration of the model in Table 4. As this model contains two continuous variables (BMlog and NDVI), only two scenarios are illustrated. The top graph shows the relationship between BMlog and MCPlog for the average NDVI for the arid zone species while the bottom graph for the average NDVI for the mesic species. The four lines stand for both sexes and both habitats. Note that the model lines for mesic and arid habitats are almost identical at an NDVI of 0.386. The measured values are shown as symbols, and only the relevant species for either habitat type are shown



appropriate food items is relatively lower and their distribution more patchy for larger animals (Harestad and Bunnell 1979; Jenkins 1981) resulting in an over-proportional increase in home range size. Supporting the resource density argument is the notion that habitat productivity is influencing home range size in some taxa. For example, the same species of

North American carnivores living at higher latitudes occupy larger home ranges than those living in more productive habitats further south (Gompper and Gittleman 1991; Lindstedt et al. 1986) and a similar effect along a gradient of aridity has been reported in Australia for marsupial macropods (Fisher and Owens 2000), feral cats (*Felis catus*) (Bengsen et al.

Table 5 Model selection for phylogenetically corrected data (pgls). Only the five most relevant models are shown

| Male model | AIC | Δ AIC | w_i | adj R ² | Female model | AIC | Δ AIC | w_i | adj R ² |
|------------------------|-------|--------------|-------|--------------------|------------------------|-------|--------------|-------|--------------------|
| BMlog + NDVI | 44.96 | 7.86 | 0.86 | 0.51 | BMlog * NDVI * habitat | 26.43 | 4.40 | 5.42 | 0.76 |
| BMlog * NDVI * habitat | 42.75 | 5.65 | 2.61 | 0.63 | BMlog + NDVI | 25.49 | 3.55 | 8.30 | 0.73 |
| BMlog + NDVI + habitat | 39.28 | 2.18 | 14.80 | 0.66 | BMlog + NDVI + habitat | 24.03 | 2.00 | 18.01 | 0.77 |
| BMlog + habitat | 37.40 | 0.31 | 37.70 | 0.68 | BMlog * habitat | 23.90 | 1.86 | 19.32 | 0.78 |
| BMlog * habitat | 37.09 | 0 | 44.02 | 0.69 | BMlog + habitat | 22.03 | 0 | 48.95 | 0.79 |

Table 6 Model parameters for the most parsimonious models for phylogenetically corrected data listed in Table 5

| Parameter | Male (BM * habitat) Value | SE | Female (BM + habitat) Value | SE |
|---------------|------------------------------|-------|--------------------------------|-------|
| Intercept | -1.878 | 0.656 | -1.948 | 0.441 |
| BMlog | 1.612 | 0.273 | 1.452 | 0.185 |
| Habitat | 0.386 * arid | 0.884 | -0.396 * arid | 0.153 |
| BMlog:habitat | -0.413 * arid | 0.297 | NA | NA |

2016) and the European fox (*Vulpes vulpes*) (Newsome et al. 2017). The present data on dasyurid marsupials support this argument as well as our third hypothesis that even in small mammals home range size scales with BM. Importantly, taxonomic affiliation could not account for the observed effect and the coefficients for the factors changed only slightly suggesting that little of the observed effect is related to phylogeny.

Of the three environmental variables tested, only average rainfall failed to improve model performance. Given the substantial year to year variations in rainfall and the extremely patchy rainfall distribution in Australia's deserts, an average figure apparently has insufficient explanatory power. Furthermore, although Habitat and study specific NDVI improved model performance significantly, the environmental signal in the present dataset appears to be not as strong as the latitudinal effect on home range size in northern hemisphere carnivores in which home range size doubled at higher latitudes (Gompper and Gittleman 1991; Lindstedt et al. 1986). Therefore, alternative strategies available to animals to overcome resource constraints have to be considered. Adjustments to population density and reduced reproductive output are independent of body size; other mechanisms are not. As such, large terrestrial animals with their low mass-specific cost of transport can engage in migration and an increase in home range size incurs fewer energetic penalties (Tucker 1970). Conversely, small species have more options to save energy partly because their mass-specific metabolic rate is much higher than that of larger species (Schmidt-Nielsen 1972). Therefore, a reduction in basal metabolic rate as documented for many smaller species from resource-poor areas or unpredictable environments (Lovegrove 2000) becomes more effective in smaller-sized animals. Moreover, the use of torpor, the most efficient energy-saving mechanism available to endotherms (Ruf and Geiser 2015), can reduce foraging requirements (Stawski et al. 2015). As far as dasyurids are concerned, population density is generally lower in arid environments than in more productive environments (Dickman 2003). Furthermore, on average, arid zone marsupials have a lower basal metabolic rates than mesic species (Withers et al. 2006). Lastly, daily torpor is well documented in dasyurids even in the larger species (Cooper and Withers 2010; Geiser 1994) and it appears that arid zone species employ torpor more frequently than their mesic counterparts (Geiser 1988; Geiser and Baudinette 1987). Interestingly, such

a difference in torpor expression can be observed even within species whose distribution range extends across a productivity gradient (Morton 1978b; Warnecke et al. 2008). As such, a number of free-ranging desert dasyurids enter torpor on almost every day during winter (Körtner and Geiser 2009; Körtner and Geiser 2011; Körtner et al. 2008; Warnecke et al. 2008). This is further augmented by basking and huddling to reduce normothermic energy requirements by up to 70% (Geiser et al. 2004; Geiser et al. 2002; Körtner and Geiser 2009; Morton 1978b; Warnecke et al. 2008). Hence, the rather moderate increase in home range size over the aridity gradient in the small-bodied desert dasyurid is likely as least partly explained by these efficient energy conservation mechanisms. Moreover, both the reduced scope for energy savings from torpor (Ruf and Geiser 2015) and the declining costs for transport (Schmidt-Nielsen 1972) with increasing BM should contribute significantly to the generally much larger scaling coefficient for home range size (> 1) compared to that for metabolic rate (~0.75).

In conclusion, our study suggests that desert dasyurids like most mammals occupy temporarily stable home ranges. This ensures familiarity with their surrounding and will likely facilitate foraging success, predator avoidance and access to daytime shelters. Nevertheless, there are indications that the quest for mating opportunities and patchy rainfall events (Dickman et al. 1995) can entail long-distance forays in some species. Whether this behaviour is more common in arid than in mesic species remains to be determined. Interestingly, home range size scales with BM with no apparent lower limit for species under 100 g, contrary to previous suggestions by Kelt and Van Vuren (2001). The consistently larger home range in male dasyurids is not simply a function of the sexual dimorphism in body size but probably a result of the generally polygamous mating system in this taxon as well as others (Bengsen et al. 2016). Importantly, the highly effective energy-saving mechanisms of torpor, basking and low BMR are apparently not sufficient to entirely compensate for the low resource availability associated with aridity, resulting in on average larger home ranges for desert species. This not only suggests that the elevated costs of transport for smaller animals still leave some flexibility in the range of movements, but also lends further support to the hypothesis that energy turnover is one, but not the only important factor that determines home range size.

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