ENERGY EXPENDITURE, WATER FLUX, AND ACTIVITY BUDGETS OF FEMALE SWAMP ANTECHINUSES IN CONTRASTING HABITATS

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Island mammals often differ behaviorally, demographically, and morphologically from their mainland conspecifics. A comparison of the water flux (WF, ml/day), daily energy expenditure (DEE, kJ/day), activity budgets, body mass, and diets of female swamp antechinuses (Antechinus minimus maritimus) from island and mainland habitats was undertaken to determine whether features associated with the island habitat influenced their physiological ecology. WF differed significantly between the 2 populations, with mainland animals having a WF 36% greater than island animals. However, there was no significant difference in DEE between individuals in different habitats (island versus mainland), although they exhibited markedly divergent behavioral patterns. Differences in diet and availability of free water for drinking may have caused the divergence in the WF values between mainland and island individuals. Although energy requirements play a key role in the spatial ecology of small mammals, other factors such as social interactions could cause observed differences in spatial organization between female A. minimus on the island and mainland.

Key words: activity, Antechinus minimus, behavior, daily energy expenditure, dasyurid, diet, doubly labeled water, island

Determining the energy requirements of free-ranging animals is of central importance to understanding the physiology and evolutionary ecology of species (Speakman 2000). For small endothermic animals, it is widely accepted that demand for energy may place proximate and ultimate controls on many behavioral and life-history attributes (McNab 1980; Thomas et al. 2001). The availability of food items in the environment may constrain the rate at which animals can acquire energy and may, therefore, be expected to have a direct influence on an animal’s energy budget (Speakman et al. 2003). Consequently, it would be expected that variations in habitat may have important effects on energy budgets of animals in the wild.

Typically, oceanic island habitats possess fewer vertebrate species, often resulting in decreased predation and interspecific competition for island vertebrates (MacArthur and Wilson 1967). These differences have been implicated in causing a cascade of demographic, morphological, and behavioral changes within island populations, often termed the “island syndrome” (Adler and Levins 1994; Stamps and Buechner 1985). Common features of the syndrome, such as niche expansion (e.g., dietary differences), insular gigantism, and behavioral modification (e.g., decreased movements), are likely to influence the availability of food items and the allocation of energy (McNab 2002). Indeed, studies comparing the resting or basal metabolic rates of birds and mammals on oceanic islands and mainland sites have commonly reported the influence of habitat (Kurta and Ferkin 1991; Magnanou et al. 2005; McNab 1994, 2002). Ecological and evolutionary changes also are expected to influence the daily energy expenditure (DEE) of island populations, which depend critically on factors such as the supply of energy and water from the environment, the food source, and its digestibility (Nagy 1987; Speakman 2000). However, there has been limited field research investigating whether insular adaptations of small mammals impact patterns of energy expenditure and water flux.

The swamp antechinus (Antechinus minimus maritimus) is a small (35- to 100-g), insectivorous marsupial (family Dasyuridae) with a restricted distribution in southeastern Australia. Large demographic and behavioral differences occur between island and mainland populations of the swamp antechinus and suggest that poorer habitat conditions may occur on the mainland. These differences may result in mainland animals expending more energy. On mainland Australia, populations are at low densities (<10 individuals/ha) and the species

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is considered rare (near threatened—Menkhorst 1995). In contrast, high-density populations (20–140 individuals/ha) occur on small offshore islands in Bass Strait, situated on the continental shelf between mainland Australia and Tasmania (Sale et al. 2006). Greater recruitment of juveniles on these islands is partly responsible for the divergence of population density (Sale et al. 2008). In addition, several behavioral distinctions occur between island and mainland populations. For example, the home ranges of individuals on the mainland were significantly larger than those of individuals from the island site (Sale and Arnould 2009). Although this supports the hypothesis of resource limitation for individuals on the mainland (Boutin 1990), similar differences in home-range size of wood mice (Apodemus sylvaticus) were not found to be linked to differences in DEE (Corp et al. 1999). Divergent temporal activity patterns also exist, with individuals on islands being predominantly nocturnal and individuals on the mainland diurnal (Sale and Arnould 2009). This also could lead to differences in energy expenditure due to exposure to different temperatures (Kronfeld-Schor et al. 2001).

In many island ecosystems, allochthonous inputs from marine-feeding vertebrates, such as seabirds, greatly increase ecosystem productivity and food availability for small mammals inhabiting these areas (Case and Schwaner 1993; Goltsman et al. 2005). For example, the availability of marine resources may allow North American deer mice (Peromyscus maniculatus) to reach high densities and to persist on small islands with low and unpredictable terrestrial productivity (Stapp and Polis 2003). Similarly, large marine inputs are likely to increase food availability for the swamp antechinus on islands in Bass Strait (Sale et al. 2006). Hence, greater food availability on island habitats may further inflate differences in the behavior and DEE of individuals between island and mainland environments.

Simultaneously analyzing physiological, behavioral, and demographic processes of small mammals living in different ecological contexts may help to understand how phenotypes are adapted to the environment and how physiological and behavioral mechanisms could constrain demographic patterns. However, there is currently little information on how differences in habitat productivity and behavioral activity budgets influence energy budgets in small vertebrates (Corp et al. 1999; Karasov and Anderson 1984; Tieleman et al. 2006), and insectivorous marsupials in particular (e.g., Green and Crowley 1989). The aims of this study were to determine the activity budgets, water flux, and daily energy expenditure of free-ranging female swamp antechinuses on a small offshore island and in an adjacent mainland habitat; and to investigate whether diet, body mass, and behavior, which commonly differ between island and mainland populations, affect divergent patterns of water flux and daily energy expenditure of animals at these sites.

**Materials and Methods**

Study sites, capture methods, and field procedures.—Individuals were captured in island and mainland habitats separated by

<20 km (Fig. 1). The mainland site was situated in an area of dense wet heath generally <3 m in height on Wilsons Promontory (38°57′S, 146°19′E) 10 m above sea level. The site was dominated by scented paperbark (Melaleuca squarrosa) and prickly tea-tree (Leptospermum juniperinum). The island site was situated on Kanowna Island (32.7 ha), located 7 km southwest of the tip of Wilsons Promontory (39°8′S, 146°20′E) in north-central Bass Strait, and was covered by dense, coastal tussock grass (Poa poiformis) < 0.5 m in height. The island is a nesting site for an estimated 100,000 pairs of short-tailed shearwaters (Puffinus tenuirostris), little penguins (Eudyptula minor), and also hosts a breeding colony of Australian fur seals (Arctocephalus pusillus doriferus). As a result of guano deposition, the island soils are nutrient rich.

Aluminium Elliott traps (10 × 10 × 30 cm; Elliott Scientific, Upwey, Victoria, Australia), baited with a mixture of rolled oats, peanut butter, and golden syrup (or honey) were used to capture live animals. Because of the large discrepancy in population densities (island, 45.7 individuals/ha; mainland,

![Figure 1](url)
2.1 individuals/ha—Sale and Arnould 2009) the size of the trapping areas differed between the 2 sites (13.1-ha and 2.4-ha grids, respectively). Body mass was recorded (± 0.1 g; Pesola AG, Baar, Switzerland) and individuals were marked using a unique pattern of nicks along the ear margin for identification. Only nonlactating females were used in the present study, because their energy expenditure, activity, and spatial organization are likely to be the result of prey resources, whereas energy use and spatial organization of males is likely to be influenced by the distribution and activity of females (Emlen and Oring 1977). In addition, the low density of males (<1 individual/ha) in the mainland habitat precluded a suitable comparison with the island habitat. Field procedures undertaken at each site were separated by 8–15 days. Environmental variables such as temperature, rainfall, and humidity can influence water turnover and energy expenditure of small mammals (Speakman 2000). However, during the study period, ambient temperature (14–18°C; Bureau of Meteorology, Melbourne, Australia) and rainfall (none recorded) conditions were similar.

Water flux (WF) and DEE of individual females (8 mainland and 14 island) were determined using the doubly labeled water technique (Lifson and McClintock 1966). This method has been previously validated by comparison to indirect calorimetry in a range of small mammals and provides an accurate measure of DEE over periods of several days (Berteaux et al. 1996b; Speakman and Krol 2005). Animals were weighed and a known mass of doubly labeled water (approximately 0.2 ml or 6 ml/kg; 30% atom 18O and 15% atom 2H) was administered intraperitoneally with a 1-ml tuberculin syringe and 1.25-cm, 25-gauge needle. Syringes with needles were weighed (± 0.001 g) before and after administration to calculate the mass of doubly labeled water injected. Individuals were placed into a container with nesting material and kept undisturbed for a 90-min equilibration period (Krol and Speakman 1999) to allow the isotopes to equilibrate in the body. They were then bled via the tail vein to obtain initial blood samples for isotopic analysis. At each site 4 animals were blood sampled without injection to estimate the background isotope enrichments of 2H and 18O (method C of Speakman and Racey [1987])). Blood samples were immediately heat sealed in 3 × 75-µl glass capillaries. The animals were then released at the site of capture and recaptured, weighed, and bled 48–72 h later, as close as feasible to whole 24-h periods (Speakman and Racey 1988) to estimate isotope elimination rates. Capillaries that contained the blood samples were vacuum distilled (Nagy 1983), and water from the resulting distillate was used to produce CO2 and H2. The isotope ratios 18O/16O and 2H/1H were analyzed using gas-source isotope ratio mass spectrometry (Isoprime IRMS and Isochrom µG; Micromass, Manchester, United Kingdom). Isotope enrichments were converted to values of DEE using a single pool model as recommended for this size of animal by Speakman (1993) assuming a Respiratory Quotient (RQ) of 0.8. There are several alternative approaches for the treatment of evaporative water loss in the calculation (Visser and Schekkerman 1999). We chose the assumption of a fixed evaporation of 25% of the water flux (equation 7.17 of Speakman [1997]), which has been established to minimize error in a range of conditions (Visser and Schekkerman 1999).

WF values (ml/day) were calculated using deuterium elimination rates (kd, per day) using the plateau calculation method and deuterium dilution spaces (Nd, ml) as a percentage of body mass (Lifson and McClintock 1966; Nagy and Costa 1980). Data were analyzed using SPSS 14.0 (SPSS Inc., Chicago, Illinois). Means are presented ± SE, and differences were considered significant at P < 0.05.

Behavioral activity and organization of individuals were determined by radiotelemetry. Although Berteaux et al. (1996a) found no evidence that carrying a radiocollar affected energy expenditure in meadow voles (Microtus pennsylvanicus), such an impact could not be discounted a priori in the present study. Indeed, radiocollars have been found to impact condition, behavior, and survivorship in other small mammal species (e.g., Tuytten et al. 2002; Webster and Brooks 1980). Furthermore, any potential impact of the radiocollars could have masked natural differences between the 2 populations. Consequently, we undertook behavioral investigations using radiotelemetry immediately following energetic investigations, that is, after the final blood sample was taken. Small, single-stage, unique-frequency radiotransmitters (151-MHz band; Sirtrack, Have lock North, New Zealand) weighing 1.5–2.0 g (<5% body mass) were fitted around the necks of individuals using a plastic cable-tie before animals were released at point of capture in both mainland and island populations. Animals were then tracked with a portable radioreceiver (Titley, Balina, New South Wales, Australia) and a 3-element handheld yagi antenna (Sirtrack) for the subsequent 3 days to determine movement patterns. To remove radiocollars, a large number of traps were deployed within the determined range area of each animal to increase the likelihood of recapture.

Locations were found by “homing in” on the radio signal. At each animal location, the coordinates were recorded to the nearest meter on a 10 × 10-m grid that covered tracking areas. Locations were mapped using a geographic information system software package (ArcView 3.3; ESRI, Redlands, California). Activity budgets (island, n = 10; mainland, n = 4) were compared by tracking individuals for 24-h periods with fixes taken every 30–45 min. Animal speed was calculated as the straight-line distance animals moved. Analyses of short-term home ranges were performed using the Spatial Analyst and Animal Movement extensions for ArcView (Hoodge et al. 1999). Home-range estimates were calculated using the Fixed Kernel method with least-squares cross validation being used as the smoothing parameter using all available fixes over at least 3 days. Techniques in the present study followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007), with approval from the Deakin University Animal Welfare Committee and Department of Sustainability and Environment Wildlife (Victoria) research permit 10003288.

Dietary analysis.—Fecal analysis is considered a reliable method for determining the diet of generalist insectivores
Table 1.—Mean (± SE) body mass (g), elimination rates $k_e$ and $k_d$ (per day), water turnover (WF; ml/day), total body water (TBW; % body mass [% BM]), and daily energy expenditure (DEE; kJ/day and kJ/g/day) for female swamp antechinuses (Antechinus minimus) on island and mainland habitats, and tests for differences between these sites.

<table>
<thead>
<tr>
<th></th>
<th>Island</th>
<th>Mainland</th>
<th>$P$</th>
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<tbody>
<tr>
<td>$n$</td>
<td>14</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>Mass (g)</td>
<td>33.7 ± 1.3</td>
<td>34.4 ± 1.6</td>
<td>0.8</td>
</tr>
<tr>
<td>$k_e$ elimination rate (per day)</td>
<td>0.9 ± 0.1</td>
<td>1.2 ± 0.1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>$k_d$ elimination rate (per day)</td>
<td>0.7 ± 0.1</td>
<td>1.0 ± 0.1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>WF (ml/day)</td>
<td>14.3 ± 0.6</td>
<td>22.5 ± 1.6</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>TBW (ml)</td>
<td>22.1 ± 0.9</td>
<td>22.2 ± 1.0</td>
<td>0.9</td>
</tr>
<tr>
<td>TBW (% BM)</td>
<td>64.4 ± 0.6</td>
<td>64.5 ± 0.6</td>
<td>0.2</td>
</tr>
<tr>
<td>DEE (kJ/day)</td>
<td>68.3 ± 1.9</td>
<td>72.4 ± 4.5</td>
<td>0.4</td>
</tr>
<tr>
<td>DEE (kJ/g/day)</td>
<td>2.1 ± 0.1</td>
<td>2.1 ± 0.1</td>
<td>0.7</td>
</tr>
</tbody>
</table>

(Dickman and Huang 1988). Scats were collected from traps, placed in 70% ethanol, and analyzed under a dissecting microscope in the laboratory. Fragments of indigestible cuticle were identified from morphological features and categorized mainly to invertebrate orders. Identification was assisted by comparisons with invertebrate reference collections and published keys. The frequency of occurrence of prey categories was defined as the number of samples in which each category was detected, expressed as a percentage of the total number of samples. Differences between samples were evaluated with chi-square tests.

Results

Body mass, total body water, and water turnover.—There was no significant difference in the body mass of females between the island (33.7 ± 1.3 g; $n = 14$) and mainland site (34.4 ± 1.6 g; $n = 8$; $t = 0.2$, $df = 20$, $P = 0.8$). Similarly, there was no significant difference in absolute total body water pool size between individuals from the island (22.1 ± 0.9 ml) and mainland (22.2 ± 1.0 ml; $t = 0.03$, $df = 20$, $P = 0.9$) or as a proportion of body mass between individuals from either habitat (island 64.4% ± 0.6%; mainland 64.5% ± 0.6%; $t = 1.2$, $df = 20$, $P = 0.2$). Minimal body weight changes (generally less than ± 2%) occurred between the time of 1st and last blood sampling.

Absolute WF differed significantly between habitats, with individuals from the mainland (22.5 ± 1.6 ml/day) having greater water turnover than individuals from the island (14.3 ± 0.6 ml/day; analysis of covariance [ANCOVA], $F = 30.4$, $df = 1$, 19, $P < 0.001$), with no significant impact of body mass as a covariate ($F = 1.8$, $df = 1$, 19, $P = 0.2$; Table 1). This difference was significant irrespective of whether body mass was included as a covariate or removed ($t = 5.2$, $df = 20$, $P < 0.001$). Likewise, mean elimination rates ($k_d$ and $k_e$) were significantly higher for individuals from the mainland ($t = 5.7$, $df = 20$, $P < 0.001$ and $t = 5.1$, $df = 20$, $P < 0.001$ for $k_d$ and $k_e$, respectively; Table 1).

Daily energy expenditure and behavioral activity.—Absolute DEE did not differ significantly between individuals from the island (68.3 ± 1.9 kJ/day) and mainland habitats (72.4 ± 4.5 kJ/day; ANCOVA, $F = 0.88$, $df = 1$, 19, $P = 0.36$) with body mass included as a covariate and habitat (island/mainland) as factors. However, there was a significant relationship between the body mass and DEE ($F = 6.2$, $df = 1$, 19, $P = 0.04$; Fig. 2). There also appeared to be an interaction between body mass and site on DEE. On the mainland site, DEE was highly positively related to body mass ($F = 14.0$, $df = 1$, 6, $R^2 = 0.84$, $P < 0.001$). However, on the island, there was no significant relationship between body mass and DEE ($F = 0.40$, $df = 1$, 14, $R^2 = 0.31$, $P = 0.56$). DEE also was significantly related (positively) to WF flux ($F = 12.9$, $df = 1$, 21, $R^2 = 0.40$, $P = 0.002$; Fig. 3). This was consistent for both the island ($F = 7.3$, $df = 1$, 12, $R^2 = 0.37$, $P = 0.02$) and mainland ($F = 10.7$, $df = 1$, 6, $R^2 = 0.64$, $P = 0.02$).

There was a significant difference between the short-term home-range size of individuals from the island and mainland (0.24 ± 0.05 ha and 1.7 ± 0.60 ha, island and mainland, respectively; $t = 3.9$, $df = 12$, $P < 0.001$). On the island, there was no significant relationship between home-range size and body mass ($F = 1.2$, $df = 1$, 8, $R^2 = 0.13$, $n = 10$, $P = 0.36$). Similar analysis for individuals on the mainland was not possible because of limited numbers. There also was no relationship between home-range size and DEE on the island ($F = 3.4$, $df = 1$, 6, $R^2 = 0.36$, $P = 0.12$) or for both sites pooled ($F = 0.01$, $df = 1$, 10, $R^2 < 0.001$, $P = 0.94$).

There was a significant difference between the distance moved between consecutive radiofixes, with mainland animals (40.8 ± 3.7 m) moving faster and over greater distances (often >100 m within 30 min) than island animals (21.3 ± 1.2 m; $F = 27.9$, $df = 1$, 291, $P < 0.001$; Fig. 4). In contrast, the activity of island animals was characterized by frequent, short shuttling movements suggesting restricted-area search patterns. A large disparity in the temporal activity patterns also
was observed between individuals on the island and mainland. Mainland animals were completely diurnal, moving distances > 80 m/h. In comparison, island individuals were mainly active during the night, generally moving 50 m/h at that time. However, many of these animals also were active during the day, generally moving 20 m/h (Fig. 4).

**Diet.**—Analysis of scats (n = 44) showed that swamp antechinuses on both island and mainland sites consumed a wide variety of prey. Because of the predominance of weevils, nonlarval Coleoptera were divided into weevils and non-weevils. Similarly, ants were distinguished within the Hymenoptera. Larval stages of Lepidoptera and Coleoptera also were separated. The most frequently represented prey types identified in scats were Coleoptera (both weevils and others), spiders (Aranaeae), invertebrate larvae (Lepidoptera and Coleoptera), earwigs (Dermaptera), and ants (Hymenoptera, Formicidae; Table 2). The frequency of occurrence of various prey differed between the 2 sites, with significant differences for earwigs, ants, pupae, and millipedes (Diplopoda; \( \chi^2 = 4.5, P = 0.03; \chi^2 = 4.3, P = 0.04; \chi^2 = 7.1, P < 0.01; \) and \( \chi^2 = 12.3, P < 0.01 \), respectively; Table 2).

**DISCUSSION**

**Water flux and total body water.**—The WF values estimated in the present study differed from allometric predictions for nonarid marsupials. WF estimates were 17% lower than predicted values on the island and 20% greater than expected on the mainland (Nagy and Bradshaw 2000). There were no significant differences between total body water as a proportion of total body mass between the sites, suggesting that there were no differences in fat stores between individuals from either habitat (Green et al. 1991). The observed differences in water turnover between individuals from the island and mainland may have been caused by dietary

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**Table 2.**—Frequency of occurrence (%) of prey items identified from analysis of swamp antechinus (*Antechinus minimus*) fecal scats from both island (n = 22) and mainland (n = 22) habitats with chi-square tests (— indicates frequency \( \leq 5 \) for differences in the frequency of occurrence of invertebrate categories between island and mainland sites. NS = not significant; * \( P < 0.05; ** P < 0.01; *** P < 0.001; \) d.f. = 1.

<table>
<thead>
<tr>
<th>Prey</th>
<th>Island</th>
<th>Mainland</th>
<th>( \chi^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coleoptera, Curculionoidea—-weevil</td>
<td>95.5</td>
<td>54.5</td>
<td>2.5</td>
</tr>
<tr>
<td>Coleoptera—excluding weevil</td>
<td>81.8</td>
<td>59.1</td>
<td>0.8</td>
</tr>
<tr>
<td>Araneae—spider</td>
<td>59.1</td>
<td>68.2</td>
<td>0.1</td>
</tr>
<tr>
<td>Coleoptera—larvae</td>
<td>59.1</td>
<td>90.9</td>
<td>1.5</td>
</tr>
<tr>
<td>Lepidoptera—larvae</td>
<td>50</td>
<td>31.8</td>
<td>0.9</td>
</tr>
<tr>
<td>Dermaptera—earwig</td>
<td>50</td>
<td>13.6</td>
<td>4.5*</td>
</tr>
<tr>
<td>Hymenoptera, Formicidae—ant</td>
<td>22.7</td>
<td>63.6</td>
<td>4.3*</td>
</tr>
<tr>
<td>Diptera—fly</td>
<td>22.7</td>
<td>31.8</td>
<td>0.3</td>
</tr>
<tr>
<td>Pupae/egg casing (order unknown)</td>
<td>54.5</td>
<td>9.1</td>
<td>7.1**</td>
</tr>
<tr>
<td>Diplopoda—millipede</td>
<td>4.5</td>
<td>68.2</td>
<td>12.3**</td>
</tr>
<tr>
<td>Blattodea—cockroach</td>
<td>4.5</td>
<td>4.5</td>
<td>—</td>
</tr>
<tr>
<td>Chilopoda—centipede</td>
<td>18.2</td>
<td>9.1</td>
<td>0.67</td>
</tr>
<tr>
<td>Collembola—springtail</td>
<td>9.1</td>
<td>41.0</td>
<td>4.5</td>
</tr>
<tr>
<td>Reptilia, <em>Egernia</em>—lizard</td>
<td>0</td>
<td>4.5</td>
<td>—</td>
</tr>
<tr>
<td>Bird feather</td>
<td>100</td>
<td>0</td>
<td>22***</td>
</tr>
</tbody>
</table>

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**Fig. 3.**—The relationship between daily energy expenditure (DEE; kJ/day) and water flux (WF; ml/day) for female swamp antechinuses (*Antechinus minimus*) on island (closed) and mainland (open) habitats before breeding (April–May). Least-squares regression equations for the island and mainland, respectively, are: DEE = 0.7 + 0.2(body mass); DEE = 22.4 + 2.3(body mass).

**Fig. 4.**—Mean (± SE) speed (m/h) of female swamp antechinuses (*Antechinus minimus*) on island (dashed; n = 10) and mainland (solid; n = 4) habitats.
differences, because invertebrate prey for insectivores vary in water content (e.g., Studier and Sevick 1992). Mainland individuals may have consumed prey with higher water concentrations, or a greater volume of such prey, in comparison to the island individuals. Alternatively, individuals from the island may have consumed prey of a higher energetic value but at a lower rate and, therefore, reduced water intake. In the present study, dietary analysis provides some equivocal support for this suggestion. Individuals from the mainland consumed a significantly greater frequency of ants and millipedes, whereas island individuals consumed a greater frequency of pupae. However, without data on the biomass of prey consumed, such conclusions should be viewed with caution.

Large differences in water turnover between short-nosed bandicoots (Isoodon macrourus) situated on island and mainland environments were attributed to individuals on the mainland drinking water (Hulbert and Gordon 1972). In our study, microhabitat differences occurred between habitats. The closed heath vegetation on the mainland occurs on poor-draining soils, contrasting to the tussock grassland habitat on the island, occurring on porous soils with high wind exposure. Therefore, the consumption of exogenous water by mainland individuals could cause the differences observed in the present study. Although the diurnal foraging and activity pattern of individuals on the mainland may lead to increased water needs due to higher ambient temperatures and greater evaporative water losses (which governs a large part of water turnover—Kronfeld-Schor et al. 2001), dasyurids generally ingest more water from their food than they need to maintain water balance (Nagy et al. 1978).

Energy expenditure and movement behavior.—Daily energy expenditure calculations for the swamp antechinus are consistent with allometric equations describing interspecific variation in DEE (determined using doubly labeled water) and body mass of nonarid marsupials (Nagy and Bradshaw 2000), insectivores (Nagy et al. 1999), and small mammals generally (Speakman 2000). DEEs calculated in the present study were within ±1 SD for all 3 allometric equations for predicting DEE. In comparison to other dasyurid species, however, DEE of the swamp antechinus in the present study (69.8 kJ/day) is lower than DEE estimates for the similarly sized (43.2-g) dusky antechinus (A. swaysoni; 128 kJ/day) and similar to the smaller (~25-g) brown antechinus (A. stuartii; 72.0 kJ/day [Nagy et al. 1978] and 65.1 kJ/day [Green and Crowley 1989]). These results suggest lower energetic costs of living for the swamp antechinus. However, the disparity between the current and previous estimates of DEE in small dasyurids may reflect differences in thermoregulatory costs because previous studies were conducted during winter (Nagy et al. 1978) or in alpine environments (Green and Crowley 1989).

An animal’s daily energy requirements are related to the size of its home range (Mace and Harvey 1983). However, few studies have found a causal link between home-range size and DEE in small mammals. In the present study, individuals on the mainland had short-term home ranges between 2 and 70 times larger in size than those of individuals on the island. In addition, individuals on the mainland moved faster and over longer distances between consecutive radiofixes than did individuals on the island. These extrinsic pressures in the mainland habitat would be expected to increase metabolism (e.g., Thomas et al. 2001). Contrary to expectations, however, the magnitude of DEE differences was low, certainly smaller than expected given the differences in home range size and animal speeds between the habitats. In the present study, the power to detect small-to-medium effects of habitat on DEE was low due to the small sample. For example, post hoc analysis revealed the power to detect a medium effect (0.15 Cohen’s $f^2$) was ~0.2. Therefore, we cannot discount the likelihood that a significant difference may exist. Nonetheless, Corp et al. (1999) also found that large differences in activity and home-range size (up to 120 times), associated with habitat (woodland versus sand-dune), did not impact DEE of wood mice. Energy involved in movement is 1 of a number of energetic costs and thermoregulation is one factor that is likely to be equally, or more, important (Corp et al. 1999; Karasov 1981). Therefore, increased locomotion costs associated with larger home ranges of these small mammals may be minimal.

The relationship between DEE and the body mass of female A. minimus differed between habitats. A significant relationship occurred on the mainland and no such relationship was recorded on the island. This could suggest that DEE is partially independent of body mass for island A. minimus. Similarly, in their study of shrews in the subfamily Crocidurinae, Magnanou et al. (2005) demonstrated partial independence of metabolism and body mass. Island shrews were heavier yet maintained the same energy (resting) requirements as lighter mainland shrews. Further detailed studies are required to determine if these metabolic differences, if indeed present, influence the unique characteristics often observed within island populations of small mammals.

Divergent temporal activity patterns between female A. minimus (diurnal versus nocturnal) were not found to impact daily energy use even though this activity would expose individuals to different environmental conditions. The nocturnally active island individuals could potentially increase energetic costs due to exposure to lower ambient temperatures, whereas the diurnally active mainland individuals could experience higher thermoregulatory (cooling) costs during periods of high ambient temperatures (Kronfeld-Schor et al. 2001). The lack of discrimination between the energy expenditure of individuals in this study is likely to reflect the mild ambient temperatures during the day and night at both sites. Activity differences of island and mainland individuals may be a predator avoidance behavior due to increased risks of diurnal raptor predation on the open tussock grassland island habitat (Sale and Arnould 2009). This habitat contrasts to the thick heath mainland vegetation, which affords greater protection.

This study demonstrated behavioral (activity patterns and movements), ecological (diet), and physiological (water turnover) differences between female A. minimus on the island and mainland, highlighting differing functional needs. However, these differences may not directly impact DEE.
Decreased home-range size, a common feature of island animals, could be a consequence of social factors, such as competitive interactions (Stamps and Buechner 1985) or the distribution of food resources, or both. These factors may limit ranging movements on the island but increase movements on the mainland. In light of the fact that only females were measured during 1 life-history stage, further investigation is required to confirm broader extension of these results.

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