

The role of diet in determining water, energy and salt intake in the thorny devil *Moloch horridus* (Lacertilia: Agamidae)

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Manuscript received June 1994; accepted October 1994.

Abstract

We examine the nutritional and digestive constraints of obligate myrmecophagy to the Australian agamid lizard, the thorny devil *Moloch horridus*. Observations of thorny devils feeding in their natural habitat, and examination of faeces collected from their habitat, confirm their essentially myrmecophagous diet. We identify two common types of ants that are eaten by thorny devils, *Iridomyrmex* sp from terrestrial trails, and *Crematogaster* sp from trails along the stems of currant bush (*Leptomeria preissiana*). Ants are consumed at a variable rate, from about 1 min⁻¹ to 12 min⁻¹. The water, energy and solute content of ants is similar to other insects; the *Iridomyrmex* sp and *Crematogaster* sp were 62% water, and contained on a dry-mass basis 28-29 kJ g⁻¹, 130-180 μmol Na⁺ g⁻¹, and 220-240 μmol K⁺ g⁻¹. The movements of thorny devils encompassed a variable area; lizards often remained within a restricted area over short periods, and did not exhibit any apparent signs of territoriality. Some lizards remained in restricted areas over considerable periods (6 months to >1 year) whereas others dispersed widely. Thorny devils were observed to be active, and feeding, over a wide range of body temperatures, and their foraging did not appear to be related to, or restricted by, any particular body temperature. The digestive assimilation of thorny devils maintained in the laboratory was only 37% for dry matter, and 59% for metabolisable energy; the expected metabolisable energy efficiency is about 70% for a generalised insect diet, but would be expected to be lower for heavily sclerotised insects, such as ants. Our analyses of the nutritional value of ants, the measured metabolisable energy efficiency, and the assumption that thorny devils consume about 750 ants per day, indicate a field water turnover rate of 0.3 ml d⁻¹, and a field metabolic rate of 2.7 kJ d⁻¹. This calculated water turnover rate is considerably lower than expected for a 35 g lizard, but is similar to that measured by radio-isotopic turnover for thorny devils in the field (Withers & Bradshaw 1995). The calculated field metabolic rate is slightly less than that predicted for a 35 g lizard, and is similar to that measured for thorny devils in the field (Withers & Bradshaw 1995). We conclude that naturally-feeding thorny devils probably consume about 750 ants per day.

Introduction

The thorny devil, or mountain devil, (*Moloch horridus*) is an extremely cryptic, slow-moving agamid lizard that is wide-spread throughout much of semi-arid and arid Australia (Greer 1989; Cogger 1992). It is a sit-and-wait predator of small ants, primarily *Iridomyrmex* spp (Saville-Kent 1897; Davey 1923, 1944; White 1947; Sporn 1955; Paton 1965; Pianka & Pianka 1970). However, little is known of the natural history, ecology or physiology of the thorny devil (Bentley & Blumer 1962; Pianka & Pianka 1970; Gans et al. 1982; Sherbrooke, 1993; Withers 1993; Heatwole & Pianka 1993; Whitten 1993), in part because it is very cryptic and difficult to study in the field.

Some other Australian lizards, particularly dragons, opportunistically consume ants but none are so exclusively ant-consumers as is the thorny devil (Pianka & Pianka 1970; Pianka 1986). Many consume termites

opportunistically, and some geckos (*Diplodactylus conspicillatus* and *Rhynchoedura ornata*) and skinks (*Ctenopus* spp) are termite specialists (Pianka 1969). Food specialisation on social insects such as ants and termites may be advantageous because the prey are a clumped and concentrated food supply, but the nutritional and energetic consequences of a restricted diet such as ants or termites have been poorly addressed even for other taxa of ant-eaters such as mammals. For example, Redford & Dorea (1984) suggested that the low nutritional value of termites and especially of heavily sclerotised ants is a disadvantage (although alates have an exceptionally high nutritional value). The nitrogen levels of ants and termites are not particularly unusual, compared to other invertebrates, but Phelps *et al.* (1975) reported a low digestibility by rats for termite protein. We are unaware of any studies which have determined for myrmecophages the digestive assimilation efficiency for either dry matter or energy.

In this study, we document the composition of the diet for thorny devils at a study site located north of Southern

Cross, Western Australia. We measure the water, energy, sodium and potassium contents for the ant fauna at this study site, and we determine the digestive efficiency of thorny devils for *Iridomyrmex* sp in the laboratory. In addition, we examined thermoregulation and movements of thorny devils. These studies enable us to evaluate possible hygric, energetic, ionic, thermoregulatory and locomotory constraints of myrmecophagy for free-living thorny devils, and to estimate values for, and ratios of, water, energy and solute turnovers.

Methods

Field Site

Thorny devils were observed and studied in the field, in a sandplain habitat (latitude 30° 17'S, longitude 119° 44'E; Fig 1) located 10-20 km north of Bungalbin, Western Australia (near fauna site 39 of Dell *et al.* 1985). The vegetation was spinifex (*Triodia scariosa* and *Plectrachne* sp) mixed with *Eucalyptus leptopoda* mallee and *Banksia elderana*, *Acacia coolgardiensis* and *Callitris preissii* tall shrubland (Dell *et al.* 1985; Beard 1990). Currant bush (*Leptomeria preissiana*; Fig 2A) was also present in the north-easterly parts of the study site. The study area is sub-desert, with warm winters (July, average monthly maximum 16-17°C) and hot summers (January, average monthly maximum 34-36°C); average annual rainfall is about 265 mm, with January-August being the wettest months (Dell *et al.* 1985).

Thorny devils were routinely captured by pit-trapping, using 0.5 m long PVC pipe pit traps (160 mm dia) and aluminium flywire fences. Individuals were also located opportunistically by walking through the study area and examining the base of currant bushes where thorny devils were often seen feeding on arboreal ants. Their faeces were collected opportunistically in the field; the characteristic size and appearance, as well as their

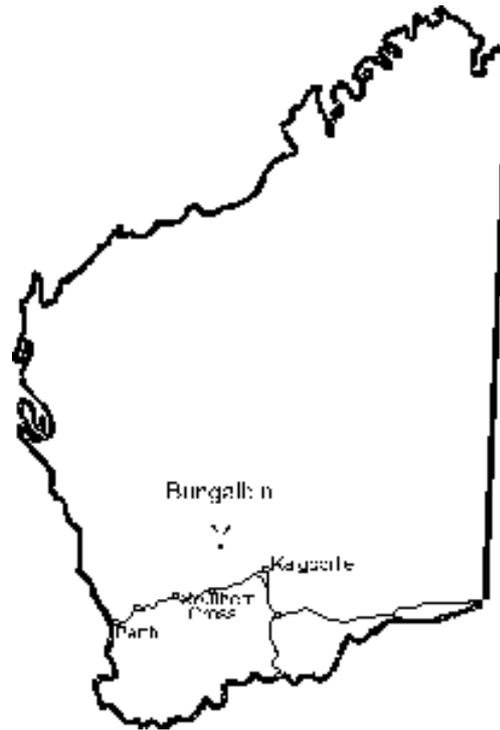


Figure 1. Location of field study site.

almost exclusive ant content, readily identified *Moloch* faeces. Faeces were often located in aggregations of 5 to 20 individual pellets.

Observations of *Moloch* feeding undisturbed at the study site enabled identification of their common ant prey as the numerous small terrestrial *Iridomyrmex* sp, as well as an ant (*Crematogaster* sp) common on currant bush. Individuals of these ant species, and numerous other species from the study site, nearby locations, and

A



B



Figure 2. A (left): Typical habitat of thorny devils in the sandplain, showing a currant bush (*Leptomeria preissiana*). B (right): Characteristic feeding posture of a thorny devil consuming ants from a trail on the trunk of a currant bush.

Perth, were sampled for identification and determination of water, energy and solute content. Ants were collected and placed in sealed plastic vials, and frozen for return to the laboratory for analysis.

Movements of thorny devils

The daily movements of thorny devils were monitored by thread spool and radiotelemetry, and longer term movements were monitored by recapture of marked (toe-clipped) individuals at the study site. A centre-unwinding nylon thread spool (Penguin Thread Company; 2 grams; \approx 270 m total length) was taped to the dorsal surface of the tail of some thorny devils. The centre-unwinding, free end of the thread was tied to a marker stake, and the lizard was able to walk unhindered by the thread trail. The length of thread that was unwound by the lizards movements was determined by following the thread and rewinding it to the current location of the lizard, then measuring the length of retrieved thread in the laboratory. This technique determines the actual daily distance moved by the lizard. Small radiotelemeters (Biotrack SS-1 one-stage; \approx 1 g) were taped to the dorsal surface of the tail of some thorny devils. These lizards were generally relocated daily using a Biotelemetry Systems radioreceiver and hand-held antenna. The actual location of the lizard was marked with a stake, and the distance and direction to the previous location were measured. Daily relocation allowed the determination of the daily point-to-point movement of lizards, and the average daily point-to-point movement over a period of 7 to 14 days. Thorny devils were marked on the abdomen using a felt-tip pen for a short-term identification, and many were marked permanently by toe-clipping.

Composition of ants

Ants were weighed individually, or in groups of 5 to 10 for smaller individuals, to \pm 0.0001 g, then oven-dried at 60°C to determine water content. The dried bodies were then analysed either for energy or solute content.

The energy content of 5 to 20 mg of dried ant bodies was determined using a microbomb calorimeter (Phillipson 1964) calibrated using oven-dried benzoic acid. It was not possible to determine the ash content of samples, so all energy values for ants are expressed as kJ per gram total dry mass.

The sodium and potassium contents of ant bodies were determined by digesting the oven-dried bodies in 0.5 to 1.0 ml of 10N nitric acid, then measuring the sodium and potassium ion contents of the digested supernatant with a Varian atomic absorption spectrophotometer, using caesium chloride as an internal standard.

Feeding trials

Thorny devils were returned to the laboratory in Perth, and fed daily with locally-collected *Iridomyrmex* ants. The lizards were housed in the laboratory in glass aquaria, with a dry sandy substrate, and a heat lamp for thermoregulation during the day. It proved impossible to feed the lizards with known numbers of weights or live ants, and so lizards were weighed to \pm 0.0001 g then placed in an aquarium containing freshly-collected ants, and allowed to feed for approximately 30 min, when they were removed and reweighed to determine the mass of

ants consumed. The thorny devils were maintained in the laboratory for 5 to 20 days in this fashion. Faeces were collected daily and oven-dried and stored for weighing and analysis of energy content.

The dry matter and energy content of the ants was determined as described above. The energy content of 0.5 to 1.5 gram samples of faeces was determined using a Gallenkamp bomb calorimeter, calibrated using benzoic acid. The ash and sand content of the faeces was determined by weighing the sample crucible before and after bombing. Energy values for faeces are presented as kJ per total dry weight (to calculate the total energy content of collected faeces) and kJ per ash-free dry weight (for comparison with the energy content of ants). The uric acid components of the faeces were included in energy determination; the "faecal" mass and energy loss therefore included material/energy that was absorbed from the digestive tract but was subsequently excreted (e.g. urine), material/energy that was not absorbed from the digestive tract but eliminated as faeces, and material/energy added to the digestive tract e.g. secretions and sloughing of the gut lining. This was done because it was considered important to determine the overall material and energy balance of the diet, for comparison with a study of field metabolic rate of thorny devils (Withers & Bradshaw, 1995).

Body Temperature

When thorny devils were located in the field, their body temperature (T_b ; °C) was measured immediately before disturbance whenever possible, using a Schultheis cloacal thermometer; air temperature (T_a ; 1 m above ground in the shade) and substrate temperature (T_s) at the site where the thorny devil was first observed were also measured.

Thorny devils were routinely maintained in the laboratory in a large circular tank (dia = 3 m), with access to a heat lamp. Body temperature was determined for devils at various times throughout the day, using a Schultheis cloacal thermometer.

Results

Diet of thorny devils

Observation of thorny devils, feeding naturally in the field, indicated that lizards typically positioned themselves over or just to the side of an ant trail, either on a sandy area or at the base of a currant bush (Fig 2B), and repetitively captured passing ants using their tongue. The ants that were observed to be eaten were invariably the common, small species; ants taken from the ground were *Iridomyrmex* sp, and ants from the currant bush were *Crematogaster* sp. The *Iridomyrmex* were readily distinguishable from *Crematogaster*, which had a very spinous trunk, with two distinctive posteriorly-directed spines on the propodeum, and a "heart"-shaped abdomen.

Feeding rates observed for thorny devils in the field varied markedly from <1 to >10 ants min^{-1} (individual values were; 0.6, 2, 2, 2, 3.3, 7.7, and 6-12 min^{-1}); mean 2.9 min^{-1} . Over short periods, however, rates up to 1 sec^{-1} were recorded; this is the maximum possible rate

because it took about 1 sec for a thorny devil to locate, capture and swallow an ant. The feeding rate appeared to vary with the abundance of ants and ambient temperature. Captive thorny devils were observed to feed at ant trails of *Iridomyrmex* spp in Perth at a rate of 0.5 to 5.8 min⁻¹ (0.5, 1.3, 1.4, 2.6, 2.9, 3.1, 3.7, 4.3, 4.5, 4.7, 5.8 min⁻¹); mean = 2.7 min⁻¹.

The faeces of *Moloch horridus* are quite distinctive, being large, ovoid and glossy in appearance; a urate pellet is frequently attached to one end of the faecal pellet (Fig 3A). The presence of essentially 100% ants in the diet is readily confirmed by visual inspection of crushed faecal pellets. Microscopic examination of faeces collected from the field confirmed the presence in the diet of small *Iridomyrmex* in localities without currant bush, and of mainly *Crematogaster* in localities with currant bush (Fig 3B). In addition, pieces of charcoal (Fig 3C) and occasionally small pieces of vegetation (Fig 3D) were frequently found in the faeces. Presumably the latter items were either ingested through mistaken identity with small black ants (*i.e.* charcoal pieces) or perhaps as items being carried by ants (*i.e.* plant material).

In addition to the common *Iridomyrmex* sp and *Crematogaster* sp consumed by thorny devils, a number of other ant species were collected from the ground and bushes at the study site, and other sites in the wheatbelt and in Perth.

Ant composition

The body mass (fresh) of ants varied considerably (Table 1), from less than 0.5 mg per individual, to over 100 mg per individual. The commonly-consumed *Iridomyrmex* (species 2) were about 0.45 mg, and the *Crematogaster* were slightly larger at 1.2 mg per individual.

The water contents of the various ants ranged from less than 50% to over 80%. There were highly significant differences in water content between the various species of ants (for species with n>2; ANOVA; F_{13,168} = 39; P<0.0005). The commonly-consumed *Iridomyrmex* 2 and *Crematogaster* sp (62% water) had an intermediate water content (Table 1). The energy content of the ants, expressed per g total weight, ranged from less than 20 to more than 30 kJ g⁻¹; the *Iridomyrmex* 2 and *Crematogaster* were intermediate, at 28 and 29 kJ g⁻¹ respectively. There were highly significant differences in energy contents of the various ant species (n>2; ANOVA; F_{13,57} = 4.8; P<0.0005). The sodium and potassium contents of the various ant species were quite variable, ranging from less than 100 to over 300 µmol g dry mass⁻¹, with highly significant differences observed between species for both sodium (n>2; ANOVA; F_{10,41} = 4.8; P<0.0005) and potassium (n>2; ANOVA; F_{10,39} = 8.5; P<0.0005). The commonly-consumed *Iridomyrmex* 2 and *Crematogaster* sp had typical sodium contents (179 and 126 µmol g dry

Table 1

Mean body mass and water, energy, sodium and potassium contents for various species of ants. The species observed to be eaten by thorny devils are indicated by an asterisk, and values are in bold face. Values are mean ± standard error, with the number of observations in parentheses.

Species	Mass mg _{wet mass}	Water Content %	Energy Content kJ g _{dry mass} ⁻¹	Sodium Content µmol g _{dry mass} ⁻¹	Potassium Content µmol g _{dry mass} ⁻¹
not identified	10.6 (2)	72.2 (2)	27.7 (1)	219 (1)	268 (1)
not identified	26.5 (2)	71.0 (2)	24.6 (1)	211 (4)	231 (1)
<i>Aphaenogaster</i> 1	1.5 ± 0.1 (4)	72.9 ± 0.6 (4)	32.0 (2)	163 (1)	195 (1)
<i>Camponotus</i> sp	8.7 (1)	66.7 (1)			
<i>Camponotus</i> sp	14.2 (2)	67.8 (2)	18.6 (1)	233 (1)	181 (1)
<i>Camponotus</i> sp	4.0 ± 0.2 (5)	68.0 ± 2.0 (5)	22.5 (2)	131 (2)	174 (2)
<i>Camponotus</i> 1	6.9 ± 0.3 (10)	65.9 ± 0.9 (10)	22.7 ± 1.9 (5)	163 ± 17 (5)	255 ± 15 (5)
<i>Camponotus</i> 2	5.35 ± 0.4 (10)	60.0 ± 0.9 (10)	24.5 ± 2.3 (7)	± 97 (2)	171 (2)
<i>Camponotus</i> 3	19.3 ± 0.8 (3)	74.1 ± 1.6 (3)	18.1 (1)	328 (1)	344 (1)
<i>Crematogaster</i> sp*	1.2 ± 0.1 (7)	62.0 ± 2.5 (7)	29.2 ± 1.2 (4)	126 (2)	216 (2)
<i>Iridomyrmex</i> sp	2.45 (2)	68.5 (2)	39.2 (2)		
<i>Iridomyrmex</i> sp	1.8 ± 0.2 (5)	53.8 ± 1.7 (5)	17.8 ± 0.9 (3)	127 (2)	149 (2)
<i>Iridomyrmex</i> 1	0.71 ± 0.03 (7)	63.2 ± 1.4 (7)	26.7 ± 1.3 (3)	213 ± 31 (3)	240 ± 36 (3)
<i>Iridomyrmex</i> 2*	0.45 ± 0.03 (13)	62.1 ± 1.4 (13)	28.1 ± 3.4 (4)	179 ± 41 (5)	241 ± 32 (5)
<i>Iridomyrmex</i> 3	0.38 (2)	68.4 (2)	22.5 (1)	237 (1)	275 (1)
<i>Iridomyrmex</i> 4	6.43 ± 0.3 (6)	70.5 ± 0.8 (6)	31.0 ± 1.0 (3)	252 ± 29 (3)	253 ± 13 (3)
<i>Iridomyrmex</i> 5	0.9 ± 0.04 (14)	65.5 ± 1.0 (12)	30.8 ± 0.7 (6)	126 ± 12 (4)	160 ± 7 (4)
<i>Iridomyrmex agilis</i>	0.77 ± 0.04 (3)	41 ± 3.2 (3)	31.5 (1)	56 (1)	40 (1)
<i>Iridomyrmex purpureus</i>	10.5 ± 0.1 (20)	70.1 ± 0.5 (20)	22.9 ± 0.9 (7)	243 ± 39 (6)	227 ± 16 (6)
<i>Melophorus</i> sp	29.1 ± 1.4 (4)	63.6 ± 2.9 (4)	22.4 (1)	101 (1)	162 (1)
<i>Meranoplus</i> sp	1.3 ± 0.1 (4)	64.4 (1)	27.1 (1)	34 (1)	43 (1)
<i>Pheidole</i> sp	0.27 (1)	51.9 (1)	21.5 (1)		
<i>Polyrachis</i> sp	12.2 ± 0.8 (20)	70.1 ± 0.5 (19)	26.0 ± 0.8 (7)	120 ± 10 (6)	162 ± 15 (4)
<i>Rhytidoponera</i>	14.9 (1)	58.4 (1)		164 (1)	167 (1)
<i>Rhytidoponera</i> 1	29.1 ± 2.1 (15)	58.5 ± 0.4 (15)	23.4 ± 0.7 (7)	115 ± 10 (6)	133 ± 13 (6)
<i>Rhytidoponera</i> 2	6.4 ± 0.6 (17)	53.4 ± 0.6 (17)	28.7 ± 1.0 (7)	115 ± 12 (5)	149 ± 9 (5)
<i>Rhytidoponera</i> 3	12.8 ± 0.5 (7)	54.9 ± 1.2 (7)	25.8 ± 0.7 (4)	108 ± 19 (3)	152 ± 9 (3)
<i>Rhytidoponera</i> 4	36.6 ± 1.5 (20)	57.8 ± 0.9 (20)	25.3 ± 1.8 (4)	115 ± 13 (6)	127 ± 13 (6)

mass⁻¹ respectively) and potassium contents (241 and 216 $\mu\text{mol g dry mass}^{-1}$ respectively).

Movements of thorny devils

The pattern of movements by thorny devils was variable; some lizards moved infrequently and for

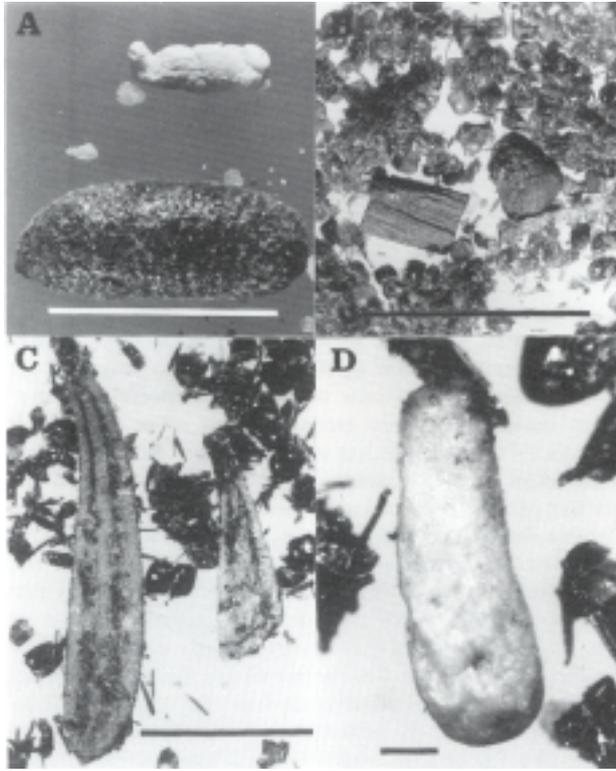


Figure 3. A: The glossy, ovoid faecal pellet of a thorny devil, showing the attached uric acid aggregate. (scale bar = 1 cm) B: Typical view of the contents of the faecal pellet of a thorny devil, showing numerous pieces of ant exoskeleton and a charcoal granules. (scale bar = 5 mm) C, D: Parts of vegetation from a faecal pellet. (scale bar = 1 mm)

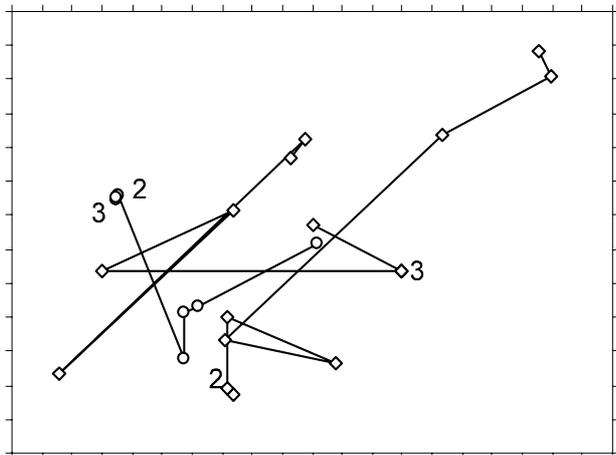


Figure 4. Pattern of movements of thorny devils. Axis tick marks are 20m intervals. Numbers next to location points (O) indicate the number of consecutive days that the lizard was located in that place (if >1).

relatively short distances (10-20 m day⁻¹) whereas others moved more often and for greater distances (>100 m day⁻¹). A few individuals moved further than the length of a nylon spool (≈ 270 m), or beyond radio-tracking range (≈ 500 m) in a single day, and are necessarily excluded from numerical analysis here. The pattern of movement of individuals (e.g. Fig 4) does not suggest any maintenance of exclusive home ranges, since the movements of many lizards overlapped those of others. Occasionally, two lizards were found together. The actual distance moved per day by thorny devils with spools was 77.9 m day^{-1} ($\pm \text{ se } 8.2$; $n=13$). The direct distance moved per day by radio-tracked thorny devils between daily relocation sites was $45.6 \text{ m point-to-point day}^{-1}$ ($\pm \text{ se } 8.6$; $n=10$). The net distance moved per day between the first and final relocation sites (determined over 7 to 14 days) was only 16.6 m day^{-1} ($\pm \text{ se } 3.9$; $n=14$). All of these values are significantly different (ANOVA, $F_{2,34} = 20$, $P < 0.001$; Newman-Keul's multiple comparison test).

A number of thorny devils were recaptured between field trips, within about 100 m of the same location, after periods of 6 months (8 individuals), about 1.5 years (3), 2 years (1), and 3 or more years (3). One had moved 0.4 km after 4 months, five had moved about 1 km after 6 months to 1 year, two had moved about 2.5 km after 4 years, and one had moved about 8 km after 1.5 years.

Digestion trials

Ten thorny devils were studied in the laboratory (body mass = $28.6 \pm \text{ se } 3.7$ g; range 15 to 52 g). The ants fed to thorny devils in the laboratory (*Iridomyrmex* 5) consisted of 65.5% water and contained 30.8 kJ of energy per g total wet weight (Table 1). The faeces of thorny devils had an energy content of $7.80 \pm 0.47 \text{ kJ g}^{-1}$ ($n=24$) expressed per total dry mass (including adherent sand particles) and $19.9 \pm 0.62 \text{ kJ g}^{-1}$ ($n=22$) expressed per ash-free dry mass. The mean ash content of faeces was very high, $37.1 \pm 1.5\%$ (24), presumably because of their high sand content, both grains within and adherent to the outside of the faecal pellet.

The thorny devils consumed ants at a rate of 0.16 ± 0.02 ($n=10$) g wet mass d⁻¹ (or 0.057 ± 0.01 g dry mass d⁻¹), which is about 0.6% of their body mass per day. This is equivalent to a total energy intake of 1.8 kJ day⁻¹. No thorny devils consumed sufficient ants per day to maintain a constant body mass; the observed weight change of -0.13 g d^{-1} ($\pm \text{ se } 0.02$) was significantly different from 0 ($t_9 = 6.5$, $P < 0.001$). However, this was significantly less ($t_{14} = 8.4$, $P < 0.001$) than the weight loss of non-feeding thorny devils of -0.30 g d^{-1} ($\pm \text{ se } 0.06$, $n=6$).

For five thorny devils, sufficient faeces were collected to enable a meaningful estimation of their steady-state energy assimilation. The total dry weight of faeces excreted over the duration of the feeding trials was $0.098 \pm 0.022 \text{ g d}^{-1}$ and the ash-free dry weight was $0.036 \pm 0.008 \text{ g d}^{-1}$. The calculated metabolisable dry matter assimilation was 37%, but the food intake was not expressed as ash-free mass whereas the faecal energy was expressed as ash-free mass (to account for its high sand and other inorganic material content). The calculated metabolisable energy assimilation was 59%, which was considerably higher than the metabolisable dry matter assimilation. The metabolisable energy intake of the

thorny devils was consequently 1.0 kJ day^{-1} (or $0.072 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$; assuming $20.1 \text{ J} \equiv 1 \text{ ml O}_2$).

Body Temperature

The mean body temperature of thorny devils able to thermoregulate behaviourally in the laboratory was $34.5 \text{ }^\circ\text{C}$ ($\pm \text{sd } 2.43$; $\pm \text{se } 0.48$; $n=26$); the body temperature data were slightly negatively skewed, with a median value of $34.0 \text{ }^\circ\text{C}$ (Fig 5).

The average for all field body temperatures recorded for thorny devils was $28.3 \text{ }^\circ\text{C}$ ($\pm \text{sd } 6.6$; $\pm \text{se } 0.7$; $n=93$), but ranged widely from $14.5 \text{ }^\circ\text{C}$ to $38.7 \text{ }^\circ\text{C}$. Mean air temperature was $25.6 \text{ }^\circ\text{C}$ ($\pm \text{sd } 5.8$; $\pm \text{se } 0.6$; $n=93$), and ranged widely from $16.0 \text{ }^\circ\text{C}$ to $40.9 \text{ }^\circ\text{C}$ (Fig 5). Mean substrate temperature was $24.5 \text{ }^\circ\text{C}$ ($\pm \text{sd } 6.5$; $\pm \text{se } 0.8$; $n=93$), and ranged widely from $14.0 \text{ }^\circ\text{C}$ to $41.7 \text{ }^\circ\text{C}$. There was a significant linear regression relationship between all T_b and T_a data, and all T_b and T_s data;

$$T_b = 4.1 (\pm \text{se } 1.8) + 0.95 (\pm \text{se } 0.07) T_a$$

($n=92$; $r^2 = 0.68$; $P < 0.001$)

$$T_b = 5.9 (\pm \text{se } 1.7) + 0.88 (\pm \text{se } 0.07) T_s$$

($n=67$; $r^2 = 0.73$; $P < 0.001$)

However, further analysis of the T_b and T_a data using two regression analysis to minimise the total residual sum of squares (Withers 1981; Yeager & Ultsch 1989; Fig 5) indicated separate relationships for $T_b < 32.5 \text{ }^\circ\text{C}$ and $T_b > 32.5 \text{ }^\circ\text{C}$; for $T_b < 32.5 \text{ }^\circ\text{C}$,

$$T_b = -0.6 (\pm \text{se } 1.8) + 1.10 (\pm \text{se } 0.08) T_a$$

($n=62$; $r^2=0.77$; $P < 0.001$)

and for $T_b > 32.5 \text{ }^\circ\text{C}$,

$$T_b = 29.5 (\pm \text{se } 1.7) + 0.20 (\pm \text{se } 0.06) T_a$$

($n=27$; $r^2=0.34$; $P < 0.001$)

At the highest T_a 's, three thorny devils were captured in or near burrows; their T_b was lower than the T_a (Fig 5).

Discussion

Our observations of the diet of thorny devils are consistent with previous reports of their essentially

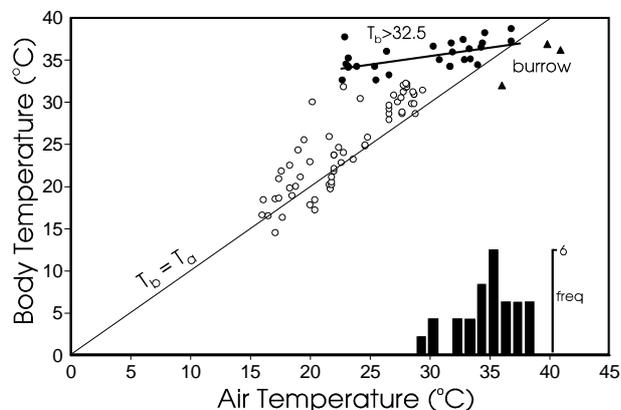


Figure 5. Relationship between body temperature and ambient air temperature for thorny devils in the field. Circles indicate data for surface active lizards; triangles are data for animals found in burrows. Closed circles and regression line are for lizards with $T_b > 32.5 \text{ }^\circ\text{C}$ (see text).

being entirely myrmecophagous (e.g. Saville-Kent 1897; Pianka & Pianka 1970). We have observed thorny devils to consume ants (*Iridomyrmex* sp) not only from terrestrial trails, but also *Crematogaster* sp from trails along the trunks of currant bushes, by standing next to or propped against the trunk with their forelegs (Fig 2B). Davey (1923, 1944) reported that thorny devils were selective for *Iridomyrmex rufoniger* over other *Iridomyrmex*, *Ectatomma*, *Monomorium*, *Camponotus*, *Polyrhachis* and *Pheidole* species. Sporn (1955) recorded that thorny devils would eat six species of non-stinging ants. Pianka & Pianka (1970) reported the contents of thorny devil stomachs to consist mainly of small (2 to 5 mg) *Iridomyrmex*, and some sticks, stones, small flowers and insect eggs, presumably ingested coincidentally with ants or by mistake.

The faeces of thorny devils are quite characteristic, being large, ovoid pellets often with an adhering uric acid aggregate (Pianka & Pianka 1970; Fig 3A). The faeces are often found in groups of a few to over twenty pellets, varying from obviously fresh to much older ones. These aggregations of faeces in special "latrine" sites occur separately from basking sites (Pianka & Pianka 1970), and indicate either the activities of a single individual over a considerable time, the combined activities of a number of individuals, or both. The faeces of thorny devils from our study localities with currant bush contained numerous fragments of *Crematogaster* sp, whereas faeces from other nearby localities without currant bush consisted of mainly fragments of *Iridomyrmex* sp. Thus, it appears that thorny devils will vary their feeding strategy and the species of ant that they feed on, depending on local conditions, but concentrate on relatively small and abundant ants which form trails. The other species of ants which we collected in the vicinity of the field site were not consumed, at least in significant numbers, presumably because of their unsuitable size, low abundance, or non-trailing behaviour.

All previous reports of feeding rates have been for captive thorny devils. Saville-Kent (1897) reported that thorny devils consumed about 1000 to 1500 *Iridomyrmex* per meal, from ant trails. Davey (1923, 1944) reported that thorny devils consumed ants at a rate of about 45 min^{-1} , in probably two meals per day lasting about 15 min each, which was sufficient to satiate the thorny devils; consequently, the ingestion of ants was about $1350 \text{ individuals day}^{-1}$. Similar rates of feeding were reported also by Duncan-Kemp (1933). In contrast, Sporn (1955) recorded thorny devils to consume 20 to 30 ants min^{-1} , with a meal lasting about 1 to $1\frac{1}{2}$ hours *i.e.* about 1875 ants per meal. We have observed a wide range of feeding rates in the field, from <1 to $>10 \text{ ants min}^{-1}$. Pianka & Pianka (1970) observed the stomachs of thorny devils to contain about 1 to 2 cm^3 (but up to 5 cm^3) of ants; typically there were about 2500 very small *Iridomyrmex*. It appears that the feeding rate, number of ants consumed per meal, length of meals, and number of meals per day might vary considerably, depending on factors such as ambient temperature, the size of the ants, and their abundance, and be higher for animals in captivity.

There were considerable differences among various species of ants in their water, energy, sodium and potassium contents. The *Iridomyrmex* 2 and *Crematogaster*

species which the thorny devils consumed were not unusual in either water, energy, sodium or potassium contents, and we suggest that the species of ants which thorny devils consume are determined more by the size, abundance and behaviour of the ants than any nutritional aspect.

Thorny devils move about 80 m day⁻¹ (spool measurements), which is fairly similar to a distance of about 50 m day⁻¹ determined by point-to-point daily; this is probably because thorny devils appear to be fairly sedentary, and move in fairly straight lines rather than meander widely. Over a period of 7 to 14 days, the thorny devils appeared to remain generally in the same area, as the long-term average point-to-point movement was only about 20 m day⁻¹ (see also Fig 4). Thus, thorny devils appear to rely on a food supply in a relatively small area, and their diet would reflect the local availability of ants (*Iridomyrmex* or *Crematogaster* spp). However, a few thorny devils were observed to move quickly over considerable distances (> 300 m d⁻¹), often essentially in a straight line; this contrasting movement pattern might reflect movements of individuals during the breeding season, or dispersing sub-adults or males. Movement records for longer periods are scarce, but the limited recapture data indicate that some individuals are extremely sedentary, even over 6 months to 3 years, whereas others had moved a kilometre or more after 6 months to 4 years.

Thorny devils were found to be active in the field over a wide range of body temperatures, as has been reported previously (Pianka & Pianka 1970; Pianka 1986). The mean of all T_b data recorded in this study was 28.3 °C (± sd 6.6; n=93), which is slightly lower than that reported by Pianka (1986) of 32.6 (± sd 4.1; n=190), at a slightly higher mean T_a of 27.1 °C (± sd 5.2). The lower T_b 's and T_a 's reported here probably reflect the considerable data obtained for thorny devils located by spooling or radiotracking when inactive e.g. at night, and during cold and rainy conditions. The linear regression relationship of $T_b = 4.6 + 0.93 T_a$ was considerably different from that reported by Pianka (1986) of $T_b = 18.1 + 0.54 T_a$, and the regressions for $T_b < 32.5$ and $T_b > 32.5$ °C had a higher and lower slope, respectively, consistent with a non-linear relationship between T_b and T_a . Thorny devils are clearly not precise thermoregulators, and are not apparently restricted by T_b in being active, or feeding. In fact, one thorny devil was observed feeding in the rain, at a T_b and T_a of 16.5 °C! At extremely high T_a , thorny devils were seen to seek shelter in burrows, a behaviour not commonly observed otherwise.

Energetics of myrmecophagy

Thorny devils and other animals that specialise on eating ants (or termites) have a spatially clumped, but locally abundant prey. Their feeding strategy is usually an initial widely-foraging search and then a sit-and-wait feeding bout. This undoubtedly has marked implications for aspects of their ecology e.g. anti-predator strategies including crypsis and defensive spines, slow movements, thermolability, extended activity period, and a stout body with a large stomach (Pianka & Pianka 1970; Pianka 1986). In addition, a highly specialised diet of ants (or termites) potentially has important digestive and nutritional implications, and determines water,

energy and ion balance. The range of water content for the various ant species (40-80%; Table 1) is similar to that reported for other ants (75-77% for *Iridomyrmex* sp; 64% for 'desert ants'; Bradshaw & Shoemaker 1967; Minnich & Shoemaker 1972), and termites and other insects (generally 50-80%; Redford & Dorea 1984). There are few values for the energy content of ants, but our values, which range from 20 to 40 kJ g_{dry mass}⁻¹ (Table 1), are typical for most biological samples (e.g. d'Oleire-Oltmanns 1977), including termites (32 kJ g_{dry mass}⁻¹; Phelps *et al.* 1975). Hubert *et al.* (1981) reported a value of 17.3 kJ g_{wet mass}⁻¹, and 16.7 kJ g_{wet mass}⁻¹ for termites; values determined here for ants range from 5 to 15 kJ g_{wet mass}⁻¹. The sodium and potassium contents of the ants varied from about 50 to 250 μmol g_{dry mass}⁻¹, and the [sodium+potassium] content from about 100 to 500 μmol g_{dry mass}⁻¹. These values are similar to those reported for desert ants of 140 μmol Na⁺ g⁻¹ and 142 μmol K⁺ g⁻¹ by Minnich & Shoemaker (1972), but are considerably lower than the values of 670 and 860 μmol g⁻¹ reported by Bradshaw & Shoemaker (1967) for *Iridomyrmex* sp consumed by the dragon *Ctenophorus ornatus*. The ash content of our ant species would be at least 1 to 2.5%, calculated from a composition of 750 μmol g_{dry weight}⁻¹ of Na⁺ + K⁺ + Cl. The ash content of termites varies from <6 to >60%, generally being higher in workers than soldiers, and higher in some species that consume soil rather than wood (Redford & Dorea 1984). Unfortunately, we were unable to determine the ash content for the ants which we studied, but presumably they are more like that of soldiers of wood-consuming species (6-10%) than workers of some geophagous species (>60%). The nitrogen content of termites is generally about 1 to 10% of dry weight (Redford & Dorea 1984).

It is widely recognised that the digestion of ants and termites is difficult, in part due to their high chitin content (Pianka & Pianka 1970; Redford & Dorea 1984; Pianka 1986). The chitin content of termites varies from 5.1% to 16.5% (Tihon 1946; Hubert *et al.* 1981), and ants are even more sclerotised than termites (Redford & Dorea 1984). The high ash content, particularly of soil-consuming worker termites, would also decrease the digestibility and energy content. Nevertheless, we are unaware of any previous studies of the digestibility of ants or termites by myrmecophages, whether amphibian, reptilian, avian or mammalian. Our laboratory feeding trials with thorny devils, although only partly successful because none of the lizards consumed sufficient food to maintain a stable body mass, nevertheless indicate a low digestibility for ants. We estimate a metabolisable assimilation efficiency of about 59%, which is considerably less than that observed for lizards eating lightly-sclerotized insects (70-89% for mealworms and 70-90% for crickets), but is similar to that measured for heavily-sclerotized adult *Tenebrio molitor* (see Harwood 1979). Bell (1990) has estimated the dry matter assimilation of a "generalised" insect to be 78%, and the metabolisable energy assimilation to be 71%, assuming a total chitin content of 12.8% of dry mass, and excretion of nitrogenous wastes and urate. Ants presumably are more sclerotised and have a higher chitin content than a "generalised" insect, and the metabolisable energy assimilation of 59% for thorny devils is expected to be lower than for a "generalised" insect.

Field Turnovers

Our studies indirectly enable the estimation of the field energy requirements of free-living thorny devils, and indicate the approximate values for water, energy, sodium and potassium turnover for free-ranging lizards (Table 2). If we accept a feeding rate of about 1500 ants per day, each weighing 0.5 mg wet weight and 0.2 mg dry weight, with an energy content of 30 kJ g_{dry mass}⁻¹ and a metabolisable energy assimilation of 60%, then the calculated field metabolic rate is 5.4 kJ day⁻¹. This is considerably more than the predicted field metabolic rate of 3.4 kJ day⁻¹ for a 35g iguanid lizard (Nagy 1982a) and the actual field metabolic rate of 2.8 kJ d⁻¹ (Withers & Bradshaw 1995; Table 2). This discrepancy could be due to our over-estimating the feeding rate of thorny devils, the energy content of their food, or the digestibility of their food. The energy content of ants determined here is similar to expected values, and the metabolisable energy assimilation of 59% does not seem unreasonably low (see above), and so the assumption of a food intake of 1500 ants d⁻¹ is the most probable error. A feeding rate of 750 ants d⁻¹ yields the observed field energy turnover rate.

The feeding rate assumed above of 1500 ants day⁻¹ would confer a field water turnover rate (ignoring metabolic water production) of 0.45 ml day⁻¹, which is considerably lower than that predicted for a 30g semi-arid/arid lizard (0.84 ml day⁻¹; Nagy 1982b) but greater than the measured field water turnover rate of 0.30 ml d⁻¹ (Withers & Bradshaw 1995; Table 2). Accounting for metabolic water production (estimated as 0.03 ml kJ⁻¹; Withers 1992) increases the calculated field water turnover rate to 0.61 ml day⁻¹. A feeding rate of 750 ants d⁻¹ yields the observed field water turnover rate.

We can also estimate the field sodium and potassium turnover rates for thorny devils. If the sodium and potassium contents of the ants are 180 and 240 µmol g_{dry}

^{mass} respectively, then the calculated turnover rates would be 54 µmol Na⁺ day⁻¹ and 72 µmol K⁺ day⁻¹ (if all dietary sodium and potassium were assimilated into the body pool). Surprisingly, this sodium turnover is less than that measured of 83 µmol d⁻¹, despite our having apparently overestimated the feeding rate. Sodium turnover has also been measured for other free-ranging lizards in order to estimate feeding rate. The field sodium turnover rate was about 1.0 to 1.2 µmol kg⁻¹ d⁻¹ for *Lacerta viridis* (Bradshaw *et al.* 1987), and 1.2 to 2.2 µmol kg⁻¹ d⁻¹ for *Ctenophorus (Amphibolurus) nuchalis* (Bradshaw *et al.* 1991). These values are similar to the calculated value of 0.8 (750 ants d⁻¹) to 1.5 (1500 ants d⁻¹) µmol kg⁻¹ d⁻¹ for thorny devils. We are unaware of any studies which have determined the field potassium turnover rate.

Although we were unable to determine the actual field water, energy and ion turnovers of thorny devils in this study, our results predict ratios of field turnover rates (Table 2). The ratio of field water turnover (WTR) to energy turnover (FMR) calculated for thorny devils is 0.11 ml kJ⁻¹ (0.61÷5.4). This ratio depends on the energy and water content of the diet, and its metabolisable energy assimilation (we assume that dietary water is 100% equilibrated with the lizard's body water pool), but not the absolute level of food consumption; it also assumes that the lizards are not able to drink in the field. Measurement of the ratio of WTR/FMR for thorny devils in the field as 0.11 ml kJ⁻¹ (Withers & Bradshaw 1995) suggests that we have correctly estimated the energy and water content of the diet, and its metabolisable energy assimilation, and that the thorny devils did not drink during the field study, although they clearly drink rain water and possibly dew when available (*e.g.* Bentley & Blumer 1962; Gans *et al.* 1982; Withers 1993; Sherbrooke 1993). The predicted ratio of WTR/FMR for a 30g semi-arid lizard is 0.25 (0.84÷3.4), suggesting that these "predicted" semi-arid lizards were drinking water.

Table 2

Field water, energy, sodium and potassium turnover rates, and ratios of rates, calculated for thorny devils from their diet, assuming a daily consumption of 1500 ants (wet mass 0.5 mg, dry weight 0.2 mg, 30 kJ g_{dry mass}⁻¹, 180 µmol Na⁺ g_{dry mass}⁻¹, and 240 µmol K⁺ g_{dry mass}⁻¹, compared with the allometrically-predicted values (for a 35 g lizard) and observed field values.

	Calculated from Diet	Predicted ¹	Measured ²
Field Turnover Rates			
WTR (ml d ⁻¹)	0.61	0.84	0.30
FMR (kJ d ⁻¹)	5.4	3.4	2.8
NaTR (µmol d ⁻¹)	54	≈60	83
KTR (µmol d ⁻¹)	72	-	-
Turnover Rate Ratios			
WTR/FMR (ml kJ ⁻¹)	0.11	0.25	0.11
NaTR/WTR (µmol ml ⁻¹)	89	≈71	277
KTR/WTR (µmol ml ⁻¹)	118	-	-
NaTR/FMR (µmol kJ ⁻¹)	10	≈18	30.2
KTR/FMR (µmol kJ ⁻¹)	13	-	-
NaTR/KTR	1.3	-	-

¹Nagy (1982a,b); Bradshaw *et al.* (1987, 1991)

²Withers & Bradshaw (1995; data for trip 4)

Acknowledgements: We are grateful to our numerous colleagues and students who assisted with these often arduous field studies of thorny devils. We sincerely thank Dr Jonathon Majer for identification of the various ants and John Dell for identification of the currant bush. We also thank Iain McLeod for assistance with ion analyses. All aspects of the study were undertaken with approval of the University of Western Australia Animal Welfare Committee and Radiation Protection Committee, the WA State Radiological Council, and the WA Department of Conservation and Land Management. A Roberts provided the photograph of the thorny devil.

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