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Short communication

Why is the marsupial kaluta, *Dasykaluta rosamondae*, diurnally active in winter: Foraging advantages or predator avoidance in arid northern Australia?



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ABSTRACT

The majority of animals have a specific activity rhythm over the 24 h daily cycle such that they can be categorised as either diurnal or nocturnal. This stability creates interest in understanding species that can invert their activity rhythm. The kaluta, *Dasykaluta rosamondae*, a small dasyurid marsupial endemic to northern arid Australia, is one such species. In contrast to most other dasyurid species and in fact most small mammals, the kaluta is almost exclusively diurnal in winter. To assess the potential benefits of diurnal activity we examined the diet and assessed potential predators and competitors. We identified 33 food categories including four classes of invertebrates, three classes of vertebrates and plant material. Diet was dominated by Coleoptera (beetles, 26.7% volume) and Formicidae (ants, 25.0% volume). We found no evidence that the prey base of kalutas differed as a consequence of diurnal activity. Likewise, diurnal foraging was probably not driven by competition. A likely explanation of diurnal activity in winter in this species is that it both allows temporal separation in activity from a significant predator, the brush-tailed mulgara, *Dasycercus blythi*, and reduces thermoregulatory foraging costs.

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1. Introduction

The majority of animal species have a specific activity rhythm over the 24 h daily cycle and as a consequence can be categorised as either diurnal or nocturnal (Kronfeld-Schor and Dayan, 2003; Vonshak et al., 2009). In general, diel activity rhythms remain consistent over time with limited seasonal variation (Kronfeld-Schor and Dayan, 2003). Exceptions to this trend occur in extreme situations such as hot or cold environments where species may invert their normal activity rhythm during the most physiologically stressful season (e.g. Lourens and Nel, 1990). The stability in activity rhythms results from differences in selection pressure faced between diurnal and nocturnal activity and the evolution of a complex set of anatomical, physiological and behavioural adaptations to enhance survival during the chosen period of activity

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(Kronfeld-Schor and Dayan, 2003).

Mammals known to change daily rhythms include heterothermic species. These mammals switch activity periods apparently to minimise thermoregulatory energetic requirements by entering a state of torpor during which body temperature and energy use are substantially reduced (Geiser and Körtner, 2010) and through behavioural adaptations such as basking to passively rewarm from torpor in sunlight (Geiser et al., 2002; Abu Baker et al., 2016). Heterothermic animals may, therefore, adjust foraging activity so that it occurs at a time that enables energy conservation through torpor and basking to be maximised. Inversion of activity patterns during the season of food limitation occurs in several species of small (<50 g body mass) carnivorous marsupial (Dasyuromorphia, Dasyuridae) from arid Australia. This group is typically strictly nocturnal (e.g. Haythornthwaite, 2005). As an example of activity rhythm inversion, a study population of fat-tailed false antechinus, Pseudantechinus macdonnellensis (20-45 g), in central Australia foraged during the day and underwent nocturnal torpor in winter (Pavey and Geiser, 2008). Individuals were also active during the



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first half of the night before entering torpor after midnight and passively rewarming by basking on sun-exposed rocks soon after sunrise (Geiser et al., 2002; Geiser and Pavey, 2007).

The kaluta, Dasykaluta rosamondae (20-40 g), a monotypic species endemic to arid northern Australia (Woolley in Van Dyck and Stahan, 2008) is even more extreme, being almost exclusively diurnal in the winter dry season (Körtner et al., 2010). Activity rhythms during the remainder of the year are not documented but it is assumed to be nocturnal. Diurnal activity rhythms were shown both by wild animals radio-tracked using implanted transmitters in winter and captive animals held at room temperature (~19 °C) at a photoperiod of LD 12:12 and later 14:10. Animals tracked in winter typically commenced activity over an hour after sunrise and returned to their burrows immediately prior to sunset before entering torpor during the night (Körtner et al., 2010). Diurnal activity in the kaluta may be selected for by a number of factors including energetically more effective foraging during the day compared to night, temporal partitioning of activity from their main predator(s) and temporal partitioning of activity from potentially competing taxa. To explore these possibilities further we investigated the diet and potential predators and competitors of the population of kaluta studied by Körtner et al. (2010).

2. Materials and methods

The study population of kaluta (average body mass $26.9 \text{ g} \pm 3.0 \text{ g}$ SE) was located near Port Hedland, north-west Western Australia ($20^{\circ}24'$ S, 118°32'E) where it occupied hummock grassland dominated by spinifex (*Triodia* spp.) on a sandplain. Animals sheltered in

burrows at night and foraged within the hummocks of spinifex during the day. Bare ground was traversed at high speed.

We assessed the presence of kalutas and other small mammals, both potential predators and competitors, by trapping with aluminium box traps (Type A, Elliott Scientific Equipment, Upwey, Australia). Traps were set over 40 days and nights from 28 May to 16 July 2008 and baited with peanut butter and rolled oats.

Scats were collected from 16 individual kalutas (12 male, 4 female) in June and July 2008. Eleven of these individuals were radiotracked and exhibited diurnal activity patterns and nocturnal use of torpor (as detailed in Körtner et al., 2010). Fifty scats were analysed from the study population. We broadly followed the faecal analysis methods outlined in Pavey et al. (2009). Prey fragments were identified to the lowest taxonomic level possible by reference to collections in the Queensland Museum, Brisbane. Further, mammal hair was collected and sent for specialist identification (Barbara Triggs, Euroa, Victoria, Australia). The volume of each prey item in each pellet was calculated by spreading all the identifiable fragments in a petri dish with graph paper underneath and estimating for each prey item the space (area) occupied by its fragments (including exoskeleton, hair, scales, feathers). Percentage volume was estimated to the nearest 5%. Taxa that contributed less than 2.5% were not included in percentage volume estimates for a given scat.

We tested for sampling completeness by generating samplebased diet component accumulation curves (1000 randomisations) using the dietary items in Table 1 run in EstimateS version 9.1.0 (Colwell, 2013). We chose the first-order Jackknife richness estimator for this purpose. The percentage of dietary sampling

Table 1

Occurrence of food categories in the diet of the kaluta, Dasykaluta rosamondae, from the Pilbara region, northern arid Australia.

Higher classification (class, order, sub-order, superfamily, family)	Prey category	Number of scats
Mammalia	Unidentified mammal	7
Dasvuridae	Unidentified dasvurid	1
Reptilia	omacinemed daby and	•
Lacertilia	Unidentified lizard	1
Aves	Unidentified bird	2
Insecta		
Blattodea	Unidentified cockroach	5
Termitoidae	Unidentified termite	32
Termitidae	Unidentified Termitidae	8
	Drepanotermes sp.	11
Orthoptera	Unidentified grasshopper/cricket	13
Caelifera	Unidentified short-horned grasshopper	1
Acridoidea	Unidentified acridoid	2
Hemiptera	Unidentified bug	1
Auchenorrhyncha	Unidentified planthopper	2
Heteroptera	Unidentified true bug	9
Coleoptera	Unidentified beetle	23
Curculionoidea	Unidentified weevil	8
Lepidoptera	Unidentified larvae	18
Hymenoptera	Unidentified wasp	3
Icheumonidae	Unidentified ichneumonid wasp	2
Mutilidae	Unidentified mutillid wasp	2
Formicidae	Unidentified ant	15
	Brachyponera	4
	Crematogaster	6
	Melophorus	1
	Monomorium	2
	Odontomachus	8
	Pheidole	1
	Rhytidoponera	8
	Solenopsis	1
Arachnida		
Aranae	Unidentified spider	13
Chilopoda	Unidentified centipede	12
Malacostraca		
Isopoda	Unidentified isopod	1
Plant	Unidentified plant	4

completeness was calculated as $S_{obs}/S_{est} \times 100$ where S_{obs} is the number of dietary categories observed, and S_{est} is the number of dietary categories estimated.

We sampled terrestrial invertebrates using pitfall traps (plastic containers, 60 mm diameter, 90 mm deep) buried flush with the ground. To preserve the invertebrates captured, we filled the traps with ethanol. We placed traps in locations where radio-telemetry had revealed that kalutas foraged. We placed a cluster of five pitfall traps in a foraging area on three occasions (20, 27, 28 June 2008). Each trap was open for 24 h.

We classified the species and higher order categories used in the text based on the Australian Faunal Directory (2015). Body mass ranges are from Van Dyck and Stahan (2008).

3. Results and discussion

We captured six species of small mammal (four rodents, two carnivorous marsupials) in addition to the kaluta. The rodent species were: sandy inland mouse, *Pseudomys hermannsburgensis*; desert mouse, *P. desertor*; spinifex hopping-mouse, *Notomys alexis*; and house mouse, *Mus musculus*. Of the carnivorous marsupials, the brush-tailed mulgara, *Dasycercus blythi* (60–110 g) is likely to be a predator of the kaluta, whereas the lesser hairy-footed dunnart, *Sminthopsis youngsoni* (8.5–12.0 g) is a potential competitor.

The prey base of the kaluta consisted of 33 food categories (Table 1). The first-order Jackknife richness estimator predicted 40.8 food categories giving a sampling completeness of 81%. Four classes of invertebrate were consumed by the kalutas: insects. Insecta (subphylum Hexapoda): isopods, Malacostraca (subphylum Crustacea); spiders, Arachnida (subphylum Chelicerata); and centipedes, Chilopoda (subphylum Myriapoda). The diet was dominated by insects (90.2% by volume, 100.0% by occurrence) (Fig. 1). Six orders of insects were consumed with the dominant groups being Coleoptera (beetles, 26.7% volume) and Formicidae (ants, 25.0% volume). The only insect larvae recorded was moth larvae which contributed 8.8% by volume. We observed kalutas twice taking processionary caterpillars of the moth, Ochrogaster lunifer. The other invertebrates contributed 7.1% by volume consisting of centipedes (5.6% by volume, 24.0% by occurrence) and spiders (1.4% by volume, 26.0% by occurrence) with isopod fragments present in a single scat (Table 1).

Kalutas in the study population also captured vertebrates, although they were not a major component of the diet (2.1% by volume). Plant material (fragments of flower and stem) was also consumed occasionally (Table 1, Fig. 1).

We captured a total of 466 invertebrates in pitfall traps over three 24 h periods (Table 2). Trap samples were dominated by ants, which comprised 74.25% of all invertebrates captured. Collembola was the next most abundant order (18.45%).

Table 2

Abundance of each invertebrate taxon sampled at foraging areas of the kaluta, *Dasykaluta rosamondae*, in the Pilbara region, northern arid Australia, expressed as a percentage of total captures (n = 466).

Order	% of total invertebrates	
Ant	74.25	
Collembola	18.45	
Araneae	1.72	
Hemiptera	1.49	
Acarina	1.29	
Diptera	1.29	
Thysanura	0.43	
Blattodea (cockroaches)	0.21	
Blattodea (termites)	0.21	
Psocoptera	0.21	



Fig. 1. Mean percentage volume of major food categories in the diet of the kaluta, *Dasykaluta rosamondae*, from the Pilbara region, northern arid Australia.

The strict diurnal activity patterns and nocturnal use of torpor of the kaluta is very rare among Australian small mammals (Croft, 2003). However, we found little evidence that the prey base of kalutas differed as a consequence of diurnal activity. Overall, the food categories consumed by kalutas in spinifex sandplain in the Pilbara are broadly similar to that of other small (<50 g) arid-zone carnivorous marsupials that are known to be nocturnal. These species include the southern ningaui, *Ningaui yvonneae* (6–14 g); Giles' planigale, Plaingale gilesi (5–16 g); fat-tailed dunnart, Sminthopsis crassicaudata (10-20 g); and stripe-faced dunnart, S. macroura (15-25 g) (Morton et al., 1983; Fisher and Dickman, 1993; Warnecke et al., 2012). If diurnal activity occurred because it provided access to a different prey base, we expected to see an increase in occurrence of diurnal vertebrates and invertebrates in the diet compared to similar-sized dasyurid species that are nocturnal. Such taxa should include predominantly diurnal invertebrates such as short-horned grasshoppers (Orthoptera, Caelifera) and diurnal vertebrates such as skinks. Despite the high level of sampling completeness (81%), we did not find this evidence. For example, a single lizard was captured and only three short-horned grasshoppers (Table 1).

The lack of a dietary explanation for diurnal foraging by kalutas is in agreement with data that show that invertebrates are not more active during the day than at night in arid regions. For example, in the Judean Desert, most arthropod taxa were nocturnal and the number of active arthropods was greater at night (Vonshak et al., 2009). These trends occurred in winter as well as in other seasons (Vonshak et al., 2009).

Diurnal foraging may allow more energetically efficient foraging by kalutas on the same prey base that would be captured at night. The use of torpor during the night, which is the coolest part of the diel cycle, maximises energy savings. Activity during the day might further reduce thermoregulatory costs particularly in winter when the risks of water loss and hyperthermia are minimal (Abu Baker et al., 2016).

Another plausible explanation for diurnal foraging in winter by kaluta is that it enables them to reduce the risk of mortality by avoiding temporal overlap with predators (Kronfeld-Schor and Dayan, 2003). Strictly diurnal activity enables kalutas to avoid encounters with the brush-tailed mulgara, a larger carnivorous marsupial that is strictly nocturnal in winter (Körtner et al., 2008) and regularly feeds on small mammals (Pavey et al., 2009). Mulgaras are known to have a suppressive impact on smaller sympatric dasyurids (Dickman, 2014) and are likely to capture and kill any kaluta encountered since the kaluta is within the mulgara's prey size range. A trapping study over a 210 ha area adjacent to our study

site carried out the year before our study (2007) estimated a density of mulgara of 0.23 per ha and of kaluta of 1.88 per ha (Thompson and Thompson, 2008). The ranges of the two species overlapped extensively in the 210 ha study area (Fig. 1 A and B of Thompson and Thompson, 2008) as they did in our study area where both species were trapped. Therefore, encounters between the two species will occur if temporal overlap occurs.

Although diurnal foraging may enable kalutas to escape from nocturnal predators, it in turn exposes them to predation from diurnally active predators. The group of predators most likely to capture kalutas during the day is visually hunting raptors that capture small, terrestrial mammals. Several diurnal raptors present at the study site have this mode of foraging including blackshouldered kite, Elanus notatus; black kite, Milvus migrans; spotted harrier, Circus assimilis; brown falcon, Falco berigora; and Australian kestrel, Falco cenchroides. It appears that kalutas minimise the risk of predation from these species by actively selecting a highly protected environment - impenetrable and closely spaced hummocks of spinifex – in which to forage (Körtner et al., 2010). Spinifex is the common name of a group of grasses that have tightly curled leaves that are spike-like in appearance and effect. No diurnal raptors are known to extract prey from mature spinifex hummocks.

A final potential explanation for diurnal foraging is that it enables kalutas to avoid overlap with a potential competitor, the lesser hairy-footed dunnart, which we trapped during the study and which is nocturnal (Haythornthwaite, 2005). However, it is unlikely that the two species compete because there are significant differences in foraging microhabitat between them. Specifically, the dunnart occupies open microhabitats when foraging with the periphery of spinifex hummocks (up to 20 cm from the edge of a hummock) being favoured (Haythornthwaite, 2005). Further, the kaluta is over twice the body mass of the dunnart (20–40 g versus 8.5–12.0 g, respectively); therefore, the relationship between the two species is more likely to be one of predator-prey rather than competitor.

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