Journal of Mammalogy, 98(3):858–866, 2017
DOI:10.1093/jmammal/gyx015
Published online March 14, 2017

Dietary flexibility in small carnivores: a case study on the endangered northern quoll, *Dasyurus hallucatus*

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The endangered northern quoll (*Dasyurus hallucatus*) is a predatory marsupial with a wide and disjointed distribution across northern Australia. The disjunct Pilbara population occurs in a uniquely arid area, and faces different threatening processes to populations elsewhere. To better understand the ecology of this small carnivore, we undertook a dietary analysis of 498 scats collected across ~100,000 km^2. We calculated dietary composition and niche breadth and modeled these against biogeophysical factors (latitude, longitude, rainfall, elevation, and distance to coast) for 10 study landscapes. We also conducted pairwise comparisons of diet groups to evaluate regional dietary differences. Quolls were highly omnivorous, consuming at least 23 species of vertebrates (mammals, birds, reptiles, frogs), as well as arthropods, molluscs, fruit, and carrion. Diet varied widely across the region, with up to 3-fold differences in dietary niche breadth between study landscapes. We found few clear environmental drivers of the diet of *D. hallucatus*. The most frequently consumed food type was insects, but their occurrence in diets decreased as that of rodents and vegetation increased, indicating potential dietary preferences. The broad and variable diet of *D. hallucatus* indicates opportunism similar to that of other small carnivores. Given this broad dietary niche, conservation managers will need a priori knowledge of local prey abundance if they are to accurately predict the composition of *D. hallucatus* diets.

Key words: arid ecosystem, biodiversity conservation, *Dasyurus hallucatus*, generalist, niche breadth, predator, small carnivore, threatened species

Human modification of the Earth's ecosystems is responsible for unprecedented species declines and extinctions (Dirzo et al. 2014). Understanding and predicting how species respond to both threatening processes and conservation actions relies on information on species' ecological traits, including diet (Hayward et al. 2006) and habitat use (Blouin-Demers and Weatherhead 2001). This knowledge is especially important for species with wide distributions that span multiple bioclimatic zones (Barbosa et al. 2012). Intra-range variation in ecological traits means that appropriate management actions may vary between locations (Garshelis and Steinmetz 2008; Killen et al. 2016). Dietary information provides insights into the ecophysiological constraints on a species, which can influence population dynamics and spatial ecology (McNab 2002). In turn, temporal or spatial changes in a species' diet may indicate environmental change (Doherty et al. 2016), or competition from sympatric species (Hayward and Kerley 2008). Thus, such information can assist in predicting the response of threatened species to environmental perturbations, such as climate change (McKinney et al. 2013).

A growing literature on intra-range variation in diets of carnivores demonstrates that carnivores often adapt their diet according to local bioclimatic pressures and prey availability (e.g., Zhou et al. 2011a; Díaz-Ruiz et al. 2013; Doherty et al. 2015; Newsome et al. 2016). Knowledge of trophic links between carnivores and their environment enables wildlife managers to understand niche requirements and develop effective conservation strategies. Small carnivores may be particularly likely to exhibit intra-range dietary variation because many species are omnivorous, consuming a range of both vertebrate and invertebrate prey, as well as plant material (Carbone et al. 1999). For example, Zhou et al. (2011a) revealed that

Holarctic martens (*Martes* spp.) consume mammals most frequently in colder northern regions, whereas plants and invertebrates are consumed most in warmer southern regions. For the wildcat (*Felis silvestris*) in Eurasia, consumption of hares was greatest at northern latitudes and consumption of reptiles, frogs, and invertebrates was highest at southern latitudes (Lozano et al. 2006).

The northern quoll (*Dasyurus hallucatus*, 240–1,120 g) is classified as Endangered under the Australian Environment Protection and Biodiversity Conservation Act of 1999 and the Western Australian Wildlife Conservation Act of 1950. This species is the smallest of Australia's quoll species, but the largest marsupial predator in northern Australia (Oakwood 2002). Once common and widespread, *D. hallucatus* has suffered considerable range contractions and population declines since European settlement in 1788 (Hill and Ward 2010). The collapse of populations in the state of Queensland and in the Northern Territory is attributed to poisoning during attempted consumption of introduced cane toads (*Rhinella marina*—Jones et al. 2014). Predation from introduced mammalian predators and habitat loss and fragmentation also threaten *D. hallucatus* across its entire distribution (Jones et al. 2014). Introduced predators (mostly feral cats [*Felis catus*] and feral dogs [*Canis familiaris*], but also red foxes [*Vulpes vulpes*] to a lesser extent) prey on *D. hallucatus*, and may compete with them for resources (Pollock 1999; Jones et al. 2014).

The western-most population of *D. hallucatus* inhabits the arid Pilbara region of Western Australia and is geographically separated from the nearest population in the Kimberley by 500 km (Fig. 1). There is no evidence of gene flow between these 2 populations, and *D. hallucatus* in the Pilbara are genetically distinct from northern quolls from the remainder of northern Australia (How et al. 2009; Westerman and Woolley 2015). The Pilbara population also has differing conservation priorities because cane toads have not yet invaded the region. A major threat to *D. hallucatus* in the Pilbara is habitat loss resulting from mining and associated infrastructure development that targets rocky habitat (Cramer et al. 2016). Improved knowledge of the ecology of *D. hallucatus* in the Pilbara, including its diet, has been identified as essential for the species' conservation (Cramer et al. 2016).

Here, we use an unprecedented data set of 498 scats collected over ~100,000 km^2 to examine variation in the diet of *D. hallucatus* throughout the arid Pilbara region. Specifically, we sought to address the following objectives:

1. Quantify the range of species and rate of occurrence of food types in diets of *D. hallucatus*;
2. Examine regional variation in dietary composition and niche breadth of *D. hallucatus*;
3. Assess how niche breadth and the consumption of food types varies according to biogeophysical factors (rainfall, elevation, distance to coast, latitude, longitude); and
4. Determine how consumption of each of the 4 most common food types (insects, vegetation, rodents, reptiles) might influence one another.

We use our findings to consider possible determinants of the diet of *D. hallucatus* and how this information can inform conservation and management.

Materials and Methods

Study region.—The Pilbara bioregion occupies 178,000 km^2 of northwestern Australia (Fig. 1) and contains coastal plains, hummock grasslands, and inland rocky mountain ranges with deep gorges. The primary land uses are pastoralism, mining, nature conservation, and indigenous reserves. Annual rainfall across the regions ranges from ~250 to 450 mm, with 70%

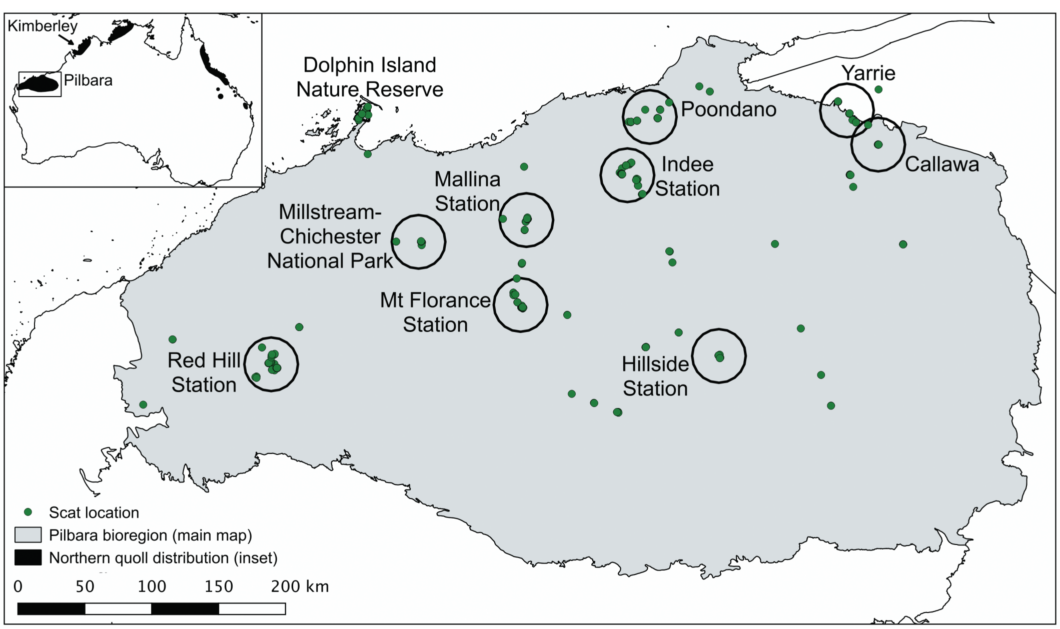

Fig. 1.—Distribution of northern quolls (*Dasyurus hallucatus*) across northern Australia (inset) and locations of scat collection (dots) in the Pilbara bioregion. The 9 circles and Dolphin Island represent study "landscapes" (see "Materials and Methods").

or more falling between December and March, mostly due to cyclonic events (Bureau of Meteorology 2016).

Scat collection and analysis.—We searched for scats in areas of rocky breakaways, mesas, gorges, and granite boulder piles throughout the study region in 2011–2015. Scats were usually found on ledges, in caves, and on top of rocks. GPS coordinates were recorded for each scat. The majority (80%) of scats were collected in the coolest months of the year (June–September) and no attempt was made to age the scats because it was not possible to reliably do this. Scats were sent for analysis to a specialist (G. Story, Scats About, Majors Creek, New South Wales, Australia) where food types were recorded for each scat and a percent volume of each food item within the scat was visually estimated using a grid system (see Supplementary Data SD1 for details).

Quantifying diets of D. hallucatus.—We grouped dietary components into 11 categories: rodents, marsupials, bats, birds, reptiles, frogs, crustaceans, molluscs, insects, vegetation, and carrion (Supplementary Data SD2). We classified as carrion any species with a body mass > 1 kg and therefore unlikely to have been preyed upon by *D. hallucatus*. Most occurrences of *D. hallucatus* hair in scats were assumed to be a result of grooming, although scats also containing *D. hallucatus* bone (but no other vertebrate remains) were classified as cannibalism, via either predation or scavenging. For individual food types (e.g., skinks, centipedes) and the 11 categories, we calculated the percentage frequency of occurrence (%FO: percentage of scats containing a certain type of food) and percentage volume of food types in scats (%VO: the volume of a certain type of food in the scats expressed as a percentage of the total volume of all food types in the scats, excluding any *D. hallucatus* in scats). The %FO may overestimate the importance of small food items that occur frequently, or species with indigestible parts that remain identifiable in scats, whereas the %VO may underestimate consumption of items that are easily digested, including soft-bodied animals such as grubs, amphibians, or geckos. It is therefore recommended that dietary studies use both metrics in order to represent the relative importance of food categories in carnivore diets (Klare et al. 2011).

Regional variation in dietary composition and niche breadth.—We created site clusters ("landscapes") at 10 locations that contained major concentrations of scats (86% of all scats). A landscape was defined as 19 or more scats situated within a central 18-km radius of similar geophysical conditions (Gibson et al. 2015; Fig. 1). The Dolphin Island landscape was defined by its coastline. We chose these parameters as a compromise between maximizing the number of samples included and creating ecologically meaningful groupings. The number of scats in each landscape ranged from 19 to 113 (mean = 43); 68 scats that did not occur within a landscape were excluded from this analysis.

We used multivariate linear models in the R package mvabund (Wang et al. 2012) to assess how dietary composition varied across the 10 study landscapes. We specified landscape as the predictor variable and a matrix of the volume of the 11 food groups in each scat as the response variables, assuming multivariate normality of errors. Multivariate *P*-values were calculated based on 1,000 residual resamples. We then used univariate tests to identify the individual food groups that differed between landscapes. To illustrate differences across landscapes, we present boxplots and mean values of the volume of each food group.

To measure dietary diversity, we used Levins' measure of niche breadth (Levins 1968), standardized on a scale from 0 to 1 (Levins' *B*) using the measure proposed by Hurlbert (1978, for formulas see Newsome et al. 2016). We measured dietary diversity using the %VO of the 11 food categories as the possible resource states. We mapped niche breadth values to illustrate regional variation.

Factors affecting niche breadth and consumption of food types.—For each landscape, we determined a centroid location by averaging the latitude and longitude (decimal degrees) of all scats within the landscape. Based on 5-km gridded data of Australia (http://spatialecology.jcu.edu.au), we calculated mean annual precipitation (mm) within the 18-km radius of each study landscape, except for Dolphin Island. Dolphin Island (32.02 km^2) fell outside of the 5-km grid, so we downloaded a point estimate of precipitation from the Atlas of Living Australia (2016) using a centroid location. Similarly, we used a 90-m digital elevation grid (http://srtm.csi.cgiar.org/) to calculate mean elevation (m) for each landscape. We used Google Earth to measure the shortest straight-line distance from each landscape centroid to the coast, rounded to the nearest 5 km.

Using general linear models (Gaussian distribution), we modeled niche breadth and food group %FO and %VO against latitude, longitude, precipitation, elevation, and distance to coast. We excluded food groups that were present at ≤ 3 landscapes (i.e., molluscs, crustaceans, and bats). We inferred statistically "significant" relationships where the 95% confidence intervals (*CI*s) of the parameter estimates did not overlap zero. All relationships described in the "Results" are statistically significant, unless stated otherwise. We present scatterplots of significant relationships. We excluded Dolphin Island from the analyses including precipitation because our initial analyses indicated that its value was an outlier (254 mm cf. 356–440 at the other landscapes) that unduly influenced the results.

Relative consumption of common food types as an indicator of dietary preference.—To assess possible preferences in the consumption of the main food groups, we used general linear models to make pairwise comparisons between consumption of insects, rodents, reptiles, and vegetation based on both %FO and %VO. We inferred "significant" effects where the 95% *CI*s did not overlap zero. Since we do not have data on the abundance of different food types, our results here are intended as a 1st step in determining possible dietary preferences.

Results

Diets of D. hallucatus.—We collected 498 quoll scats from 325 locations in the Pilbara bioregion (Fig. 1). We recorded at least 16 mammal species as prey or carrion in the scats, as well as birds, skinks, dragons, varanid lizards, geckoes, snakes, frogs, invertebrates, and plant material (Supplementary Data SD2). The mammal prey species were 3 rodents: *Zyzomys argurus*, *Pseudomys delicatulus*, *Pseudomys hermannsburgensis*; 5 dasyurid marsupials: *Dasykaluta rosamondae*, *Sminthopsis youngsoni*, *S. macroura*, *Ningaui timealeyi*, *Pseudantechinus* sp.; and 2 bats: *Rhinonicteris aurantia*, *Nyctophylus* sp. (Supplementary Data SD2). Carrion species were *Trichosurus vulpecula*, *Macropus rufus*, *M. robustus*, *F. catus*, *Canis* sp., and *Bos taurus* (Supplementary Data SD2). About 18% of scats contained *D. hallucatus* hair assumed to be ingested during grooming, but on 8 occasions (1.6% occurrence) the additional presence of bones, but no identifiable remains from other vertebrate species, suggested cannibalism either from predation or scavenging. The invertebrates recorded in scats were molluscs, crustaceans, beetles and bugs, grasshoppers and crickets, ants and termites, caterpillars and cocoons, centipedes, spiders, millipedes, and scorpions (Supplementary Data SD2). *D. hallucatus* frequently consumed seeds, fruit, flowers, and other plant material (29% of scats; Supplementary Data SD2). Native figs (*Ficus* spp.) accounted for 10% of these (probably primarily *F. aculeata*). Other fruiting species were *Passiflora* sp. (probably *P. foetida*), Myrtaceae spp., *Scaevola spiniscens*, *Goodeniaceae* spp., and *Cassytha* spp.

Of the 11 food categories, insects were consumed most frequently, followed by vegetation, reptiles, rodents, birds, crustaceans, molluscs, carrion, marsupials, bats, and frogs (Supplementary Data SD2). Insects contributed the greatest to overall scat volume, followed by vegetation, rodents, reptiles, birds, crustaceans, marsupials, carrion, bats, molluscs, and frogs (Supplementary Data SD2). The most frequently consumed insect groups were ants and termites, followed by beetles and bugs, grasshoppers and crickets, grubs and caterpillars, centipedes, spiders, cocoons, millipedes, and scorpions (Supplementary Data SD2).

Regional variation in dietary composition and niche breadth.—Dietary composition differed amongst landscapes ($F_{9,420}$ = 35.67, P = 0.001). Consumption of rodents (based on mean scat volume) was highest at Callawa, Hillside, and Yarrie ($F_{9,420}$ = 4.98, P = 0.006; Fig. 2). Bats were only consumed at Mallina, Poondano, and Yarrie ($F_{9,420}$ = 2.83, P = 0.045; Supplementary Data SD3). Consumption of birds was highest at Callawa, Hillside, and Red Hill ($F_{9,420}$ = 3.80, P = 0.024; Fig. 2). Consumption of reptiles was highest at Hillside, Indee, Millstream, and Mt Florance ($F_{9,420}$ = 3.09, P = 0.038). Consumption of insects varied greatly across landscapes, with the highest consumption at Millstream and Mt Florance, and lowest at Callawa, Poondano, and Yarrie ($F_{9,420}$ = 3.62, P = 0.028). Vegetation was consumed in the greatest volumes at Poondano and least at Hillside and Millstream ($F_{9,420}$ = 3.82, P = 0.024). Crustaceans were only consumed at Dolphin Island, Mallina, and Yarrie ($F_{9,420}$ = 6.53, P = 0.001). Molluscs were only consumed at Callawa and Dolphin Island ($F_{9,420}$ = 3.34, P = 0.032). Consumption of marsupials ($F_{9,420}$ = 1.04, P = 0.621), carrion ($F_{9,420}$ = 0.68, P = 0.715), and frogs ($F_{9,420}$ = 1.94, P = 0.163) did not vary according to landscapes (Supplementary Data SD3). Dietary diversity (Levin's niche breadth) varied widely across the region, from a minimum of 0.10 at Mt Florance to a maximum of 0.33 at Callawa (Fig. 3). Niche breadth for the entire region was 0.21.

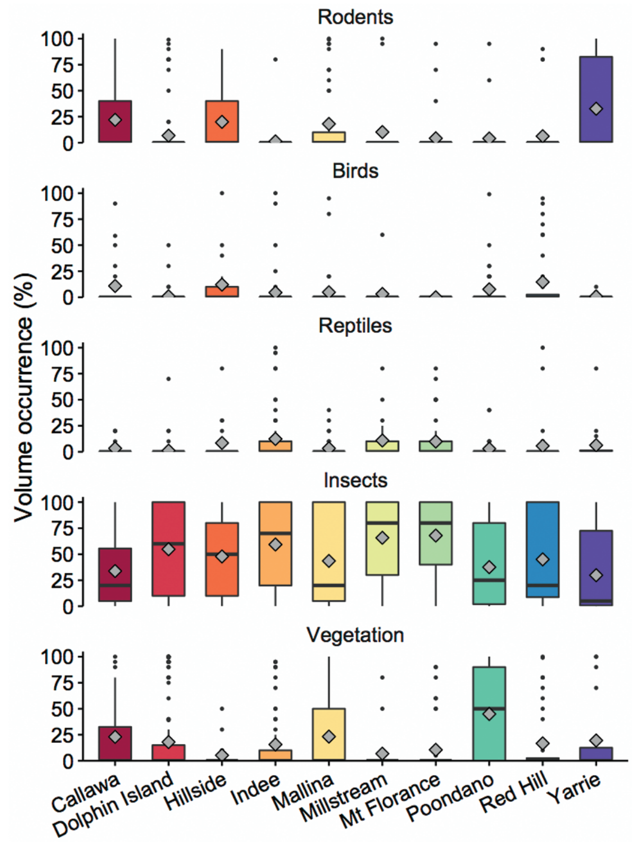

Fig. 2.—Boxplots of the percentage volume of the 5 most common food groups in the diet of northern quolls (*Dasyurus hallucatus*) at 10 study landscapes in the Pilbara region, Australia (see Fig. 1). Gray diamonds represent mean values. See Supplementary Data SD3 for boxplots of rarely consumed food groups (marsupials, bats, carrion, frogs, crustaceans, and molluscs).

Factors affecting niche breadth and consumption of food types.—The %VO of insects decreased with longitude, but %FO did not (Fig. 4; Supplementary Data SD4). The %VO and %FO of both rodents and marsupials increased with longitude (Fig. 4; Supplementary Data SD4). Similarly, the %VO and %FO of both rodents and marsupials increased with precipitation, although the relationship was not significant for rodent %FO (Fig. 4; Supplementary Data SD4). Vegetation %VO and %FO increased with latitude and decreased with elevation and distance to coast, although the %FO relationships were not significant for latitude and distance to coast (Fig. 4; Supplementary Data SD4). Both carrion %VO and %FO increased with distance to coast (Fig. 4; Supplementary Data SD4). All other relationships between food groups or niche breadth and biogeophysical variables were not statistically significant (Supplementary Data SD4).

Relative consumption of common food types as an indicator of dietary preference.—There was an inverse relationship between the %VO of insects at a landscape with that of

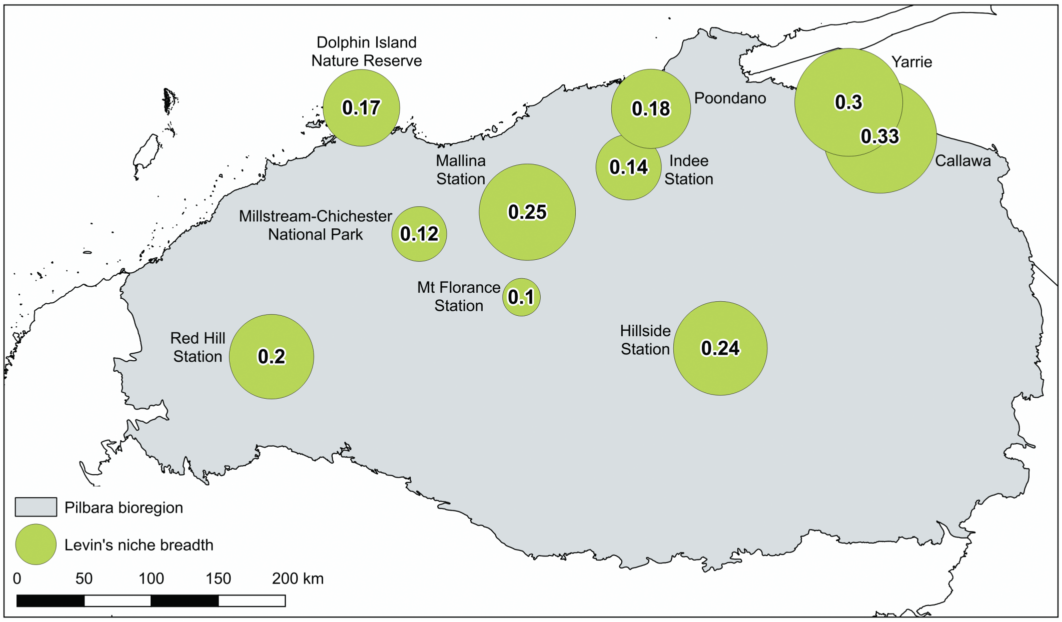

Fig. 3.—Regional variation in the dietary diversity (Levin's niche breadth) of northern quolls (*Dasyurus hallucatus*) in the Pilbara region, Australia. Circles are scaled proportionally; a larger circle indicates higher dietary diversity.

rodents and vegetation. The volume of reptiles consumed at a landscape-scale increased with that of insects and decreased with that of vegetation (Table 1; Fig. 5). There were no significant relationships with the %FO of any group or the remaining %VO comparisons (Table 1).

Discussion

Our broad-scale analysis demonstrates that northern quolls in the arid Pilbara region of northern Australia are omnivorous. Insects, vegetation, small mammals, and reptiles appeared to be the most important food groups. This result is similar to previous studies from tropical northern Australia (Oakwood 1997; Pollock 1999; Radford 2012). The occasional occurrence of food items, such as bats and molluscs, illustrates the range of food items consumed. Diet of *D. hallucatus* varied widely across the region, with up to 3-fold differences in niche breadth between landscapes. However, there appeared to be few clear broad-scale environmental drivers of *D. hallucatus* diet. Dietary niche breadth was not correlated with any biogeophysical variables, nor was the occurrence of many food groups.

The broad and variable diet of *D. hallucatus* is similar to that of other small carnivore species elsewhere (Zielinski and Duncan 2004; Murphy et al. 2005; Zhou et al. 2011b). For instance, the diet of the American marten (*Martes americana*) in California was also dominated by rodents and insects, while plants and birds also were common (Zielinski and Duncan 2004). Similar dietary flexibility in small carnivores such as stoats (*Mustela erminea*), American mink (*Neovison vison*), and mongooses (*Herpestes javanicus*) has allowed them to successfully invade a broad spectrum of bioclimatic niches across the globe (Long 2003). As discussed below, the diet of *D. hallucatus* may be driven by the local availability of different food types, rather than bioclimatic gradients per se.

Insects form a major component of the diet of *D. hallucatus*, but their volume in the diet decreases as that of rodents increases. Insectivory is a common feeding strategy for small carnivore species—comprising nearly 70% of the dietary volume of the similarly sized meerkat, *Suricata suricatta* (500–800 g—Doolan and Macdonald 1996)—but becomes unsustainable as body size increases (Carbone et al. 1999). Previous studies of dasyurid carnivores indicate that prey size is positively correlated with predator body mass, suggesting that larger prey items are preferentially pursued (Fisher and Dickman 1993; Glen and Dickman 2006). Insects are small and contain a high proportion of indigestible chitinous exoskeleton, so are likely to be less preferred than rodents. Although it may be more energy intensive for quolls to catch rodents than insects, this is likely offset by greater reward because *D. hallucatus* would need to eat fewer rodents for a single meal (Griffiths 1980; Pavey et al. 2009). Less time spent foraging should decrease the risk of predation for *D. hallucatus*, especially from feral cats, which are typically nocturnal (Bradshaw et al. 2012) and have temporal overlap with other quoll species (Fancourt et al. 2015).

Optimal foraging theory suggests that animals choose prey types based on the trade-off between costs and benefits that provide the maximum net benefit to the individual (Perry and Pianka 1997). Abundance of prey items, their ease of capture, handling time, and other nutritional factors can all influence foraging decisions (Davies et al. 2012). The difference in *D. hallucatus* diet between different landscapes and habitats (e.g., island and mainland) indicates that there are different foraging strategies occurring. Animals on Dolphin Island consumed crustaceans in a greater volume than rodents and reptiles, despite the presence of a variety of vertebrates on the island, including abundant rock rats (*Z. argurus*; J. A. Dunlop, pers. obs.). While rock rats are presumably more energy-rich food items than crustaceans,

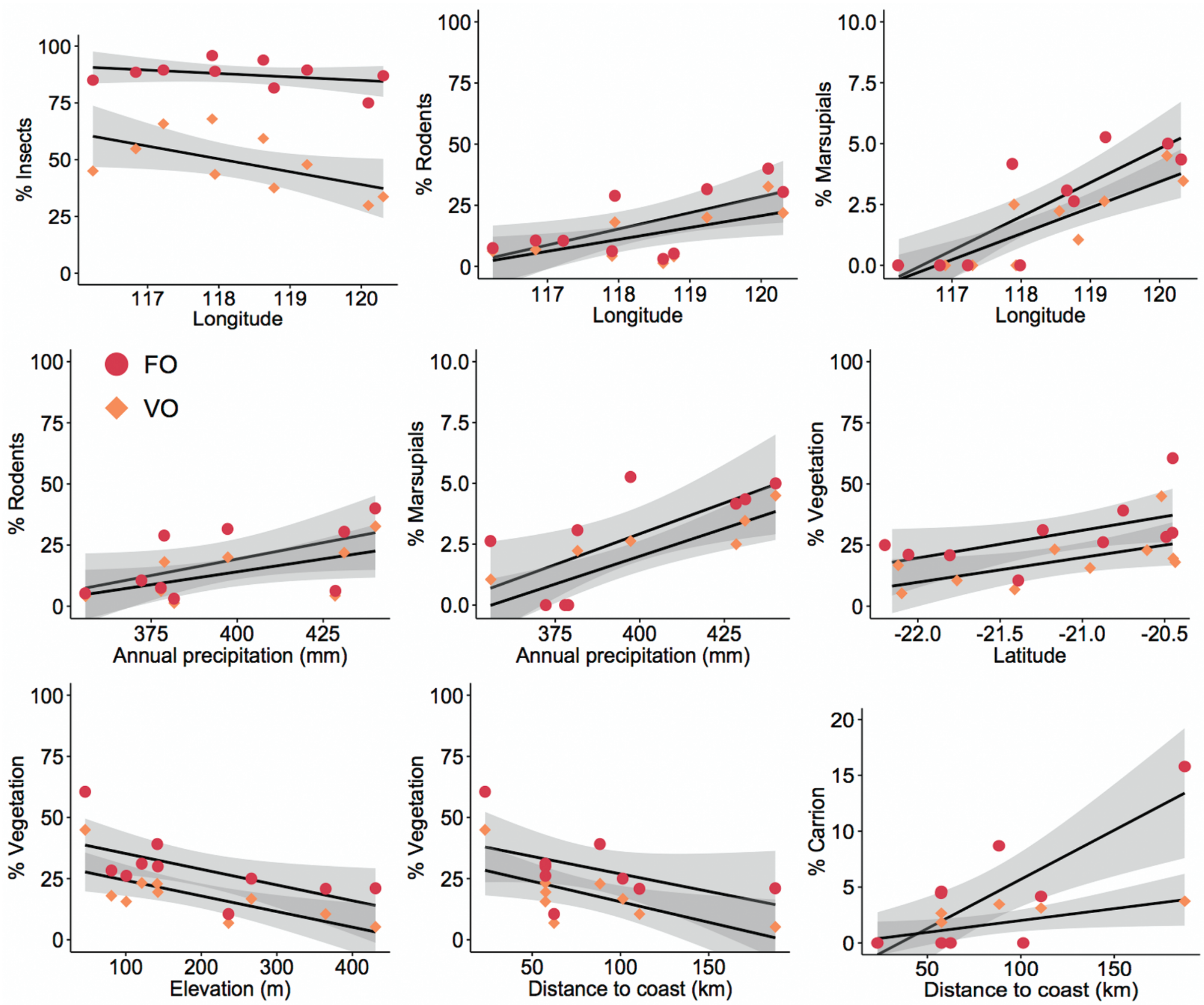

Fig. 4.—Relationships between food groups consumed by northern quolls (*Dasyurus hallucatus*) and biogeophysical variables in the Pilbara region, Australia. The black lines represent fitted relationships from generalized linear models and the gray shaded areas are 95% confidence bands. Red circles represent %FO and orange diamonds represent %VO. Different scales have been used on the y-axes to aid interpretation. %FO = frequency of occurrence; %VO = volumetric occurrence.

Table 1.—Results of general linear modeling for relationships between the occurrence of 4 main food types (insects, rodents, reptiles, vegetation) in diets of northern quolls (*Dasyurus hallucatus*) in the Pilbara. %FO = frequency of occurrence; %VO = volumetric occurrence. Bold text indicates significant relationships, i.e., the *CI*s do not overlap zero.

Food group	Parameter values	Insects	Rodents	Reptiles
%FO				
Rodents	Estimate	−1.11		
	95% *CI*	−2.50, 0.29		
Reptiles	Estimate	0.51	0.04	
	95% *CI*	−0.44, 1.46	−0.40, 0.48	
Vegetation	Estimate	−1.04	−0.01	−0.61
	95% *CI*	−2.41, 0.34	−0.68, 0.67	−1.58, 0.37
%VO				
Rodents	Estimate	**−0.51**		
	95% *CI*	**−0.91, −0.11**		
Reptiles	Estimate	**0.18**	−0.08	
	95% *CI*	**0.02, 0.34**	−0.34, 0.17	
Vegetation	Estimate	**−0.50**	−0.10	**−1.83**
	95% *CI*	**−0.98, −0.02**	−0.87, 0.66	**−3.42, −0.24**

there are likely to be greater energy costs involved in capturing rock rats (Calver et al. 1988). This discordance between the representation of food types in the environment and the diet is common for generalist carnivore species. In central China, the yellow-throated marten (*Martes flavigula*) displayed a preference for fruits over rodents when both were at peak abundance,

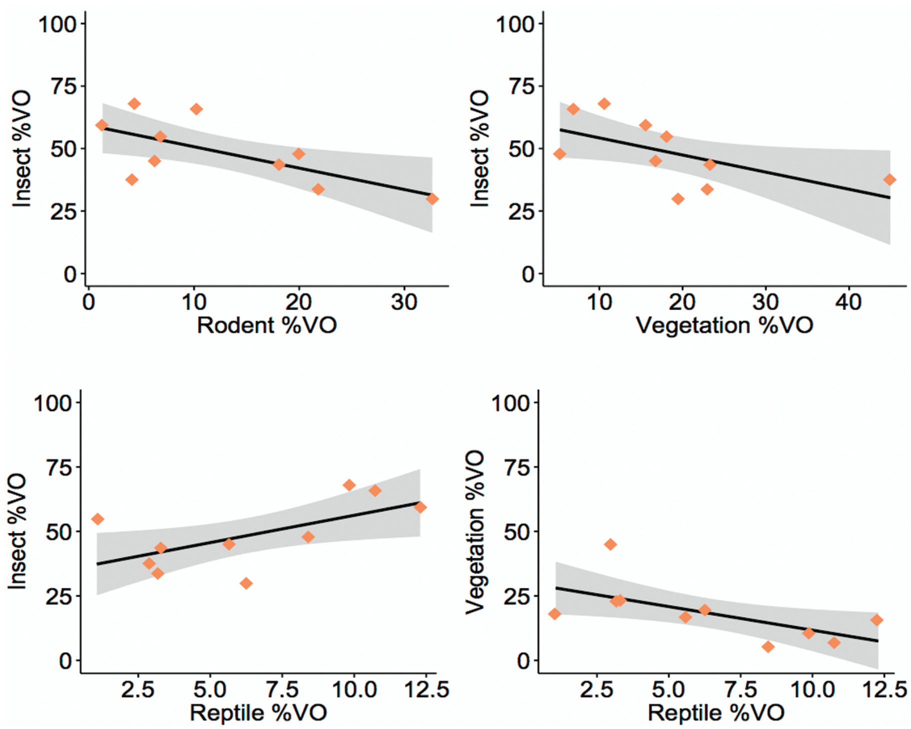

Fig. 5.—Relationships between food groups (%VO) consumed by northern quolls (*Dasyurus hallucatus*) in the Pilbara region, Australia. The black lines represent fitted relationships from general linear models and the gray shaded areas are 95% confidence bands. %VO = volumetric occurrence.

but switched to rodents when both food types were least abundant (Zhou et al. 2011b). It appears that crustaceans form a staple in the diet of *D. hallucatus* on Dolphin Island, irrespective of abundance of other prey, although this requires further investigation across all seasons, including estimation of prey availability.

Conservation implications and future studies.—The opportunistic and omnivorous feeding habit of *D. hallucatus* means that conservation managers are unlikely to be able to predict dietary composition without a priori knowledge of local prey abundance. This highlights the challenges faced when trying to conserve threatened species that have disjunct populations across varied bioclimatic zones (e.g., Barbosa et al. 2012; Peterman et al. 2013). Nonetheless, the importance of rodents in the diet at mainland sites suggests that reductions in rodent abundance may have negative consequences for *D. hallucatus*. Small- and medium-sized mammals have suffered precipitous declines in northern Australia since at least the 1990s due to predation by feral cats, livestock grazing, changed fire regimes, and interactions between these threats (Ziembicki et al. 2014). The status of Pilbara mammals is not well understood, but if rodents become less abundant, we may observe a shift in diets of *D. hallucatus*. Future studies could seek to determine whether *D. hallucatus* experiences dietary competition from feral cats, for which rodents are an important prey item (Doherty et al. 2015).

The presence of species much larger than quolls in their diet confirms that they occasionally scavenge food, which raises the possibility that smaller species consumed by *D. hallucatus* also may have been scavenged rather than preyed upon. Scavenging by quolls may have implications for feral cat control programs that aerially deploy toxic 1080 (sodium fluoroacetate) sausage baits across the landscape (Morris et al. 2016). Although *D. hallucatus* has some resistance to the toxin due to the natural occurrence of fluoroacetate in native *Gastrolobium* plants, the small size of *D. hallucatus* makes them vulnerable to poisoning if they consume several baits (King 1989; Jones et al. 2014). Preliminary experimental evidence indicates that while *D. hallucatus* will opportunistically consume baits, they appear to eat them incrementally and have not been recorded to suffer a lethal effect (R. Palmer, WA Department of Parks and Wildlife, pers. comm.), although further studies are needed.

Some scats contained seeds likely to be from *Passiflora foetida*. This is an invasive weed of environmental concern that is common in the Kimberley and Northern Territory, but currently found in low numbers in Pilbara creeklines (Keighery 2011; Lyons et al. 2014). If seeds remain viable after digestion, northern quolls may be vectors for the spread of this weed. *D. hallucatus* also consumed greater volumes of vegetation at landscapes where they consumed lower amounts of insects and reptiles. We hypothesize that small vertebrates are a high-value and preferred food source, and diet-switching to fruits common in rocky habitat may result from competitive exclusion of quolls from spinifex grasslands by feral cats (Hernandez-Santin et al. 2016).

Although fecal microscopy has been evaluated as a reliable method for dietary analysis of insectivorous mammals, some soft-bodied taxa may be underrepresented in fecal pellets (Dickman and Huang 1988). Frogs occurred in 1.41% of scats; however, analysis of gut contents of *D. hallucatus* by Oakwood (1997) revealed that more than 60% of animals had consumed frogs. Thus, our scat analysis may underestimate the occurrence of frogs in diets of *D. hallucatus* in the Pilbara. Nonetheless, the presence of frogs in *D. hallucatus* scats in the Pilbara confirms their propensity to eat cane toads (O'Donnell et al. 2010), which are predicted to naturally colonize the region within the next 50 years (Tingley et al. 2013).

Seasonal differences in diets of *D. hallucatus* in the Pilbara may be revealed if future surveys collect scats during the hottest and wettest part of the year (December–March—Oakwood 1997). However, wet-season fieldwork in the Pilbara is logistically challenging due to reduced accessibility. As a consequence of our study, we recommend that future research should: 1) investigate how diet of *D. hallucatus* varies seasonally and inter-annually, particularly in relation to their highly seasonal breeding cycle; 2) quantify dietary preferences by collecting data on both diet and prey abundance; and 3) target unsurveyed areas, including a greater range of islands.

Acknowledgments

The authors acknowledge R. Ellis for providing northern quoll scats; J. Lees for assisting with processing scats; G. Story for undertaking the scat analysis; and T. Newsome, R. Palmer, A. Glen, and an anonymous reviewer for their helpful comments on earlier versions of the manuscript. This work was financially supported by environmental offsets and public good funds provided by BHP Billiton, Rio Tinto, Atlas Iron, Fortescue Metals Group, Roy Hill, Process Minerals International, and Main Roads Western Australia.

Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Methods for scat analysis.

Supplementary Data SD2.—Frequency of occurrence (%FO) and percentage volume (%VO) of food items contained in 498 scats of northern quolls (*Dasyurus hallucatus*) in the Pilbara.

Supplementary Data SD3.—Boxplots of the percentage volume of rarely consumed food groups in the diet of northern quolls (*Dasyurus hallucatus*) at 10 study landscapes in the Pilbara region (see Fig. 1).

Supplementary Data SD4.—Generalized linear modeling results for the effect of biogeophysical variables on the frequency of occurrence (%FO), volumetric occurrence (%VO), and dietary niche breadth of diets of northern quolls (*Dasyurus hallucatus*) in the Pilbara.

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Submitted 2 August 2016. Accepted 24 February 2017.

Associate Editor was Chris Pavey.