The truth about cats and dogs: assessment of apex- and mesopredator diets improves with reduced observer uncertainty

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Dietary (scat) analysis is a key tool for assessing the potential effects of predators on prey and for comparing resource use between predators, information that is crucial for effective wildlife management. However, misidentification of the species from which scats originate could result in inaccurate conclusions regarding predator–prey interactions and their consequences for ecosystems, which may ultimately compromise conservation and management actions. To address this issue, we developed a framework for decision-making in the face of uncertain scat species origin by incorporating field, laboratory, and molecular identification techniques. We used the framework to examine the diets of two predators, a native apex predator (dingo, *Canis lupus dingo*) and an invasive mesopredator (feral cat, *Felis catus*), from 696 field-collected scats in the arid zone of Australia. We examined how uncertainty regarding scat species origin changed perceptions of the nature of the relationship between coexisting predators and their prey. The extent of dietary overlap between dingoes and cats varied with the method used to identify scat species origin. Dietary overlap assessed by laboratory identifications was twice as high as when uncertainty in scat species origin was resolved through our decision framework. If uncertainty in scat species origin is not resolved in dietary studies, practitioners and decision-makers relying on this information run the risk of making misinformed conclusions regarding the ecological function of predators (including potential impacts on threatened species), which could have perverse outcomes if the wrong predators are targeted for management. With uncertainty in scat species origin resolved through our decision framework, a low level of dietary overlap between the two predators was demonstrated, and medium-sized mammals most threatened with extinction were shown to be more at risk of impact from feral cat than from dingo depredations.

Key words: apex predator, *Canis lupus dingo*, critical weight range, diet, *Felis catus*, intraguild competition, invasive species, mesopredator, scat analysis, uncertainty

Competitive suppression by dominant apex predators can lead to decreased growth, fecundity, or survivorship of smaller-bodied mesopredators (Ritchie and Johnson 2009). Such regulation results from competition for shared resources such as prey (exploitation competition) or through the persecution or killing of the smaller predator by the larger (interference competition, intraguild predation—Polis and Holt 1992; Ritchie and Johnson 2009). These interactions can ultimately lead to a reduction in abundance or a change in behavior of the smaller predator so that encounters with the larger predator are minimized (Brook et al. 2012). For example, African wild dogs (*Lycaon pictus*) are kept at low densities by competition with spotted hyenas (*Crocuta crocuta*), and by competition with and predation by lions (*Panthera leo*—Creel and Creel 1996). Egyptian mongooses (*Herpestes ichneumon*) and common genets (*Genetta genetta*) have been shown to avoid areas used by Iberian lynx

(*Lynx pardinus*), which are known to harass and occasionally kill them (Palomares et al. 1996).

Although definitive evidence of intraguild competition can only be obtained from removal experiments, dietary studies can assess the likelihood and potential severity of competition between two predators (Mac Nally 1983). High levels of dietary overlap can indicate an increased likelihood for exploitation or interference competition, contingent on the resource being in limited supply. Therefore, understanding the diets of predators and the extent of dietary overlap can be an important tool for assessing the ecological function of predators and ultimately for guiding integrated, multispecies management (Fedriani et al. 1999; Doherty and Ritchie 2017). For instance, in conservation programs, it may be desirable to control certain predators to minimize their impacts on target threatened species and assist species recovery. However, predator removal can have unanticipated cascading effects on other trophic groups (Prugh et al. 2009; Ruscoe et al. 2011). Understanding the potential for competitive interactions between predators can help avoid unpredicted or unintended outcomes from management actions (Zavaleta et al. 2001; Doherty and Ritchie 2017).

Analysis of scat contents is particularly useful for assessing diets because this method does not rely on direct observation or capture of live individuals, which can be difficult for predators that are elusive, difficult to detect, or occur in low densities (Wilson and Delahay 2001). However, distinguishing among the feces of sympatric, similar-sized predators can be difficult even for trained observers, a fact highlighted by studies that have evaluated the accuracy of putative field identifications using molecular genetic methods (see Table 1). However, these molecular techniques are not always successful in assigning species identification to scats (Murphy et al. 2000) and can be prohibitively expensive and impractical for many situations (Prugh and Ritland 2005). As a result, many studies continue to rely on trained field observers to assign species identity to scats without explicitly accounting for or acknowledging potential bias from misidentifications (Monterroso et al. 2013). Identification errors could result in inaccurate conclusions regarding predator–prey interactions, foodweb structure, and community ecology, which may ultimately compromise wildlife conservation and management (Morin et al. 2016).

Invasive predators are a major driver of species declines (Salo et al. 2007; Doherty et al. 2016) and many management programs seek to reduce their impacts through targeted control methods. Among the most harmful invasive predators globally, the feral cat (*Felis catus*) and red fox (*Vulpes vulpes*) have had particularly severe impacts on the native biota of Australia (Woinarski et al. 2015). Because feral cats and foxes often consume small- to medium-sized prey rarely larger than their own body weight, they have had particularly strong impacts on native mammals falling within what has been termed the critical weight range (CWR) for extinction risk—between 35 and 5,500 g (Burbidge and McKenzie 1989). Reducing the abundance or activity of feral cats and foxes is critical to the

Table 1.—Selected studies showing the accuracy of mammalian carnivore scat identifications made by trained observers in the field compared to identification of those scats using molecular DNA techniques; n = number of putative scats successfully extracted and amplified for DNA sequencing.

Putative field identification	n	Accuracy (%)	Inaccuracy (%)	DNA-identified species	Study location
Red fox[a] (*Vulpes vulpes*)	157	86.3			Spain
			7.7	Stone marten	
			1.7	European wildcat	
			4.3	Dog	
Stone marten[a] (*Martes foina*)	126	77.8			Spain
			20.4	Red fox	
			1.9	Pole cat	
European wildcat[a] (*Felis silvestris*)	37	11.5			Spain
			84.6	Red fox	
			3.9	Stone marten	
Snow leopard[b] (*Panthera uncia*)	49	42.9			China, India, and Mongolia
			38.8	Red fox	
			4.1	Wolf/dog	
Pine marten[c] (*Martes martes*)	86	54.7			Scotland, England, and Wales
			44.1	Red fox	
			1.2	Pole cat	
Mink[d] (*Neovison vison*)	45	0			Scotland
			47.0	Pine marten	
			41.0	Red fox	
			6.0	Otter	
			3.0	Pole cat	
			3.0	Stoat	
Coyote[e] (*Canis latrans*)	647	92			Alaska
			8.0	Non-coyote	

[a]Monterroso et al. (2013).
[b]Janečka et al. (2008).
[c]Davison et al. (2002).
[d]Harrington et al. (2010).
[e]Prugh and Ritland (2005).

conservation and recovery of many CWR mammals (Doherty et al. 2017). Arriving in Australia ~200 years ago at the time of European settlement, the feral cat's adaptability and hunting success coupled with human-aided dispersal across the continent, has resulted in a ubiquitous distribution (Abbott 2008; Denny and Dickman 2010) that is broader than that of the red fox, which only occurs across the southern two-thirds of the continent (Woinarski et al. 2015).

Increasing evidence suggests that the dingo (*Canis lupus dingo*), the top terrestrial predator in Australia, may benefit certain native CWR mammals through the suppressive control of smaller mesopredators including feral cats (Glen et al. 2007; Johnson et al. 2007; but see Hayward and Marlow 2014). However, the dingo is largely regarded as a pest throughout much of Australia for actual or perceived impacts on livestock (Fleming et al. 2001), and control programs involving exclusion fencing, poison baiting, shooting, or trapping are widely employed across the continent (Corbett 1995; Fleming et al. 2001) with many jurisdictions requiring landholders to undertake canid control programs. Additionally, there is some evidence of dingoes preying on threatened mammal species within the CWR (Allen and Leung 2012). However, dingoes occur throughout most of Australia in ecosystems as diverse as alpine grasslands to desert grasslands, and their diet varies accordingly (Fleming et al. 2001; Davis et al. 2015). Effective management of dingoes should be context dependent and consider their ecological function in the management area. Scat analysis informs managers about the identity and quantity of dietary items taken by predators (Klare et al. 2011) and can therefore provide a tool for understanding the relative threat posed by each predator to prey species and for examining resource use between sympatric predators. Such analyses can be severely compromised if the identity of predator scats cannot be reliably assigned.

Here, we develop a framework for decision-making in the face of uncertain scat species origin, which incorporates field, laboratory, and molecular identification techniques to resolve uncertainty in scat identities. We use the framework to examine the diets of dingoes and feral cats from field-collected scats in the Australia's arid zone and examine how uncertainty in scat species origin might change perceptions of the nature of the interaction between an apex predator and an invasive mesopredator. With these results, we explore the consequences of misguided perceptions about predator identity for conserving native Australian CWR mammals and managing sympatric predators. Finally, with scat species origin resolved through our decision framework, we examine the potential for interspecific competition between dingoes and feral cats using dietary overlap estimation and explore the relative possible impact that each species poses to mammals of conservation concern, specifically, native CWR mammals.

Materials and Methods

Study area.—The study was conducted on a 2,410-km² indigenous protected area (IPA) known as Matuwa (formerly Lorna Glen cattle station) located in the northern Goldfields region of Western Australia, 842 km northwest of the state capital, Perth (26.23°S, 121.56°E; see Fig. 1). Matuwa was destocked in 2003 and cattle are largely absent from the site but occur frequently on surrounding properties where cattle production is still active. The region is a hot arid desert, receiving highly erratic and unreliable rainfall averaging 259 mm annually. Average maximum daily temperatures range from 19.4°C in winter to 39°C in summer. Vegetation communities are composed primarily of hummock grasslands and open woodlands. Dingoes and feral cats co-occur in the region and are common at the study site; the non-native red fox also occurs at the site but is rare and infrequent. A feral cat control program has been active at the IPA since 2003 and has had some success in reducing cat abundance at the site through annual application of toxic sodium monofluoroacetate Eradicat baits (Algar et al. 2013). At the time of this study, the IPA was co-managed by the Department of Parks and Wildlife (Parks and Wildlife) of Western Australia (now the Department of Biodiversity, Conservation and Attractions) and the Wiluna Martu Aboriginal community, and is the site of an ongoing restoration program with 11 species of small- and medium-sized mammal species targeted for reintroduction (Dunlop and Morris 2009).

Field and laboratory methods.—Diets of feral cats and dingoes were investigated from 696 scats collected opportunistically while driving along the 852 km of vehicle dirt tracks located on the study site from April 2013 to November 2014. Due to extreme high temperatures during the summer months, fieldwork was restricted; hence, no scats were collected between December and February. During scat collections, tracks were
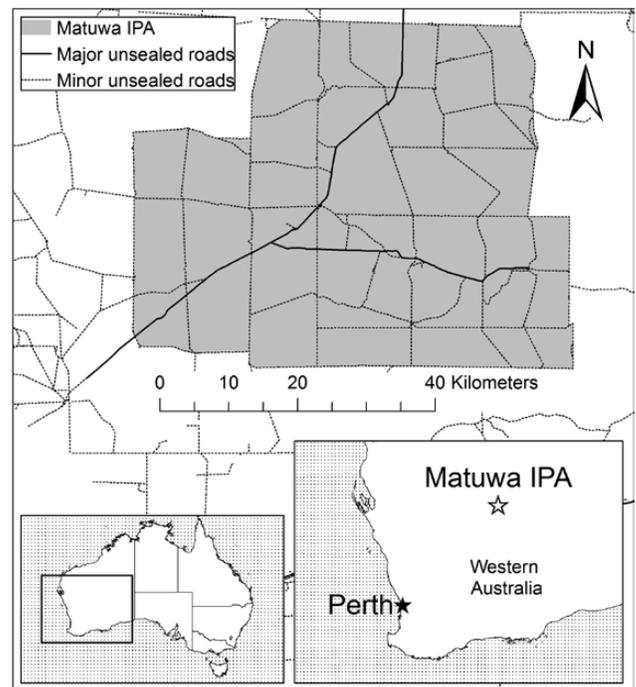

Fig. 1.—Location of Matuwa indigenous protected area (IPA) in the semiarid interior of Western Australia. Total area of the reserve is 2,410 km² and includes 852 km of unsealed vehicle tracks along which scat collections were made.

driven at an average speed of 25 km/h allowing both the driver and front passenger to scan the track and side vegetation for scats or latrine sites. A single scat was defined as one or more fecal pellets that were deposited in the same spot. Scats were collected in small paper bags, labeled with the location and date of collection, and then sent to a specialist laboratory for analysis of contents (http://www.scatsabout.com.au). Prior to shipment to the laboratory, a small amount of material (< 0.1 g) was scraped from the outer part of the scat, the portion likely to contain mucosal cells of the animal as it passes through the digestive tract (Kohn and Wayne 1997), and retained for genetic analysis. All research was approved by the University of Western Australia and the Western Australian Department of Biodiversity, Conservation and Attractions Animal Ethics Committees; methods conformed to the guidelines of the American Society of Mammalogists (Sikes et al. 2016).

To process scats, samples were oven-dried at 100°C for 12 h to kill any parasites and then weighed. Next, the samples were placed in individual nylon bags and washed for 15 min in a washing machine which left only indigestible prey fragments (Johnson and Aldred 1982). Prey contents were identified to the most specific and accurate taxonomic level possible through comparison with known reference material or the literature (Watts and Aslin 1981; Triggs and Brunner 2002) and hair was identified following the technique described by Brunner and Coman (1974). Typically, mammals were identified to species, reptiles to family or suborder, and arthropods to order or class. Birds were identified only as ratite, which included one species, the emu (*Dromaius novaehollandiae*), or non-ratite.

Scat identification and the decision framework.—Initial identification of scat species origin was made in the field and assigned a certainty score of either definite or likely depending on the collector's confidence in assigning the correct species to the scat. Scat identifications were typically based on morphological characteristics and the manner in which the scats were deposited (Triggs 2004). For example, compared to dingo scats, cat scats tend to be smaller in size with pinched-off ends and are typically deposited in sandy soils or leaf litter where they are partially or fully buried. Many of the scats identified as cat were collected on tracks in sandy patches directly on or just adjacent to tire ruts and were found by looking for either bury piles or partially exposed scats, and occasionally, for recently deposited scats, identifying the distinctive starfish-shaped burying pattern cats create. On the other hand, dingo scats tend to be larger in size, contain larger bone fragments, and are usually deposited on elevated places such as on rocks or vegetation around prominent features or track intersections. Scats identified as dingo were typically collected adjacent to or slightly off of tracks and around intersections or large trees. Both cats and dingoes tend to use the same sites more than once and the discovery of one scat often lead to more.

Despite the different scat characteristics of each species, uncertainty in identification can arise due to factors such as: 1) range in size of each predator (some large cats are bigger than small or juvenile dingoes), 2) site disturbance, 3) time since deposition and degradation due to weather or the actions of other wildlife, and 4) experience of and amount of information available to the observer. Therefore, because dingo and cat scats can appear similar and scat identification can be challenging (Glen et al. 2011; Doherty 2015), we requested that the laboratory conducting the contents analysis also identify the scat species origin, and, like the field collections, assign a certainty of classification as definite or likely based on their confidence in ascribing the correct species to each particular scat. While field identifications had the advantage of context and scat placement to aid identification, laboratory identifications had the advantage of using morphology and scat odor, which was released upon heating during scat processing (G. Story, Scats About, Majors Creek, New South Wales, Australia, pers. comm.). Dingo and feral cat scats typically have strong and distinctive odors that are often used as a basis for identification (Triggs 2004).

To identify and resolve potential discrepancies in scat species origin, we developed a decision framework to assist with scat identifications (Fig. 2). By incorporating components of genetic analysis, classifications of observer certainty, and rates of observer error, the framework allowed us to reduce uncertainty at various steps in the process. In the first stage of the decision framework, scat species origin is identified, first in the field and then in the laboratory, by two independent, trained observers with strong backgrounds and experience in Australian field ecology who also assign a classification of certainty to quantify the confidence of their identification. If the two observer identifications are consistent, then the scat is classified according to identity and no further classification is carried out. Any inconsistencies in identifications between the two observers are flagged as uncertain. If DNA has been retained from the scat, these uncertain identifications are resolved using genetic molecular testing following the method of Berry and Sarre (2007). This method involves a real-time polymerase chain reaction (PCR) procedure using species-specific primers and melt-curve analyses of fragmented DNA strands to test for the presence of fox, cat, or dingo. The quantity of the DNA present in the sample is approximated by calculating a cycle threshold (ct) value, the point at which DNA amplification exceeds a consistent threshold, where a lower ct value indicates a higher DNA concentration and a difference of 3.33 in ct value indicates a 10-fold difference in the amount of DNA present. Ct values below 25 provide the best chance of obtaining an individual identification via microsatellite DNA analysis. The results of the genetic testing were sometimes conflicted, often presenting a strong and weak signal. We assumed the weak sample was the result of contamination and used the strong signal as the identifier of scat species origin when the difference in initial DNA present, based on ct values, was greater than two orders of magnitude.

Finally, if DNA has not been retained, genetic amplification fails, DNA testing is unavailable (e.g., due to budget restrictions), or the results remain conflicted, uncertainty is then resolved using observer certainty scores with the species identity of that scat defaulting to the more certain observer. If both observers are equally certain, then in the next stage observer
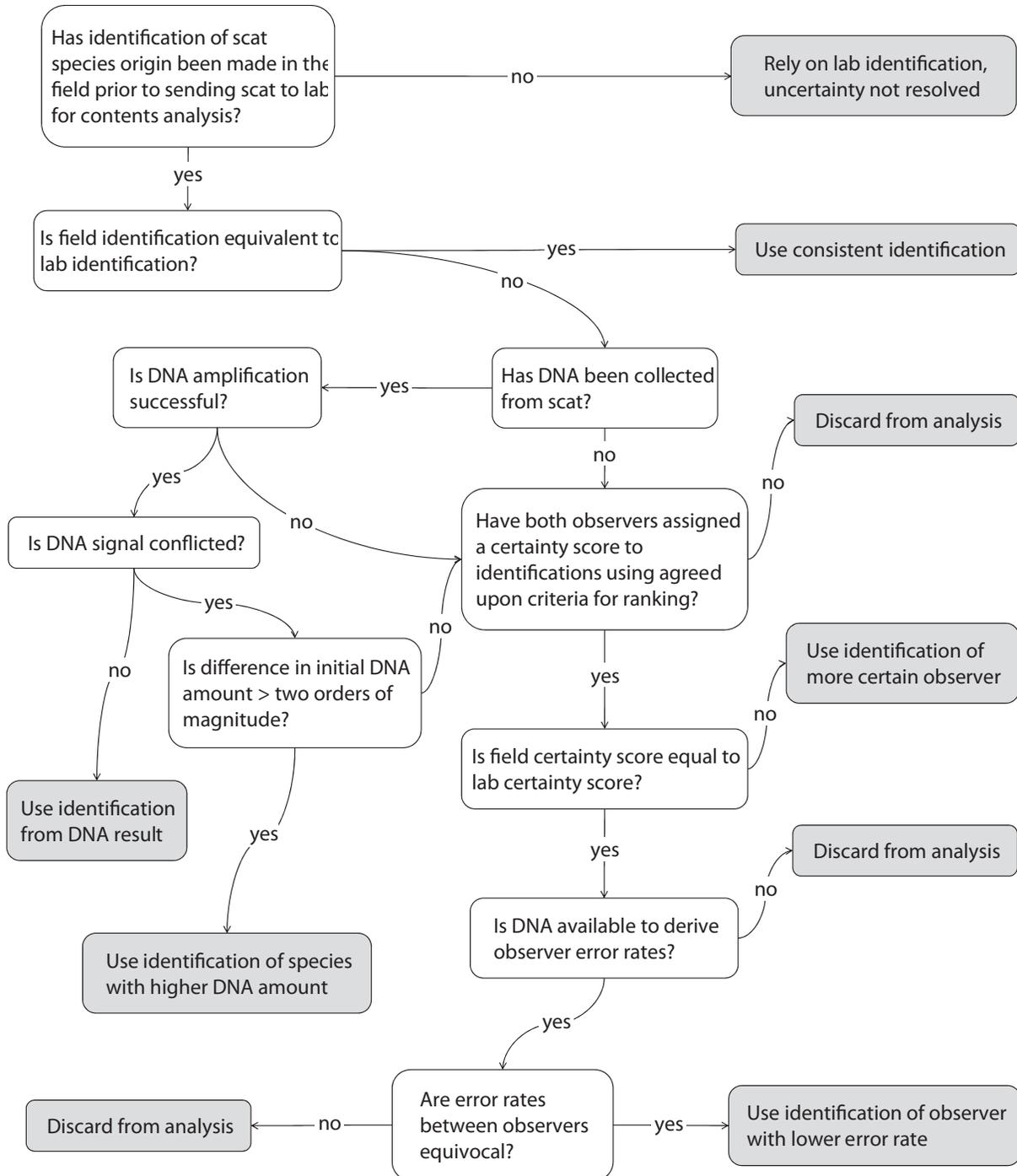
Fig. 2.—Decision framework used to resolve uncertain identifications of scat donor species for samples collected at Matuwa indigenous protected area (IPA), Western Australia.

error rates are calculated from a subset of genetically tested scats and the species identity of the scat is determined from the observer with the lower error rate (Fig. 2).

To examine how uncertainty in scat species origin could influence perceptions about the relationship between dingoes and feral cats, we calculated estimates of dietary overlap from putative field and laboratory identifications. We then compared these estimates of dietary overlap to the estimate of dietary overlap calculated using the scat species origin resolved through the decision framework and evaluated differences between all three estimates of dietary overlap using bootstrapped confidence intervals (*CI*s). We used principal component analysis (PCA) to visually examine the difference in dietary overlap under scenarios using field-identified scats, laboratory-identified scats, and scats where species origin was resolved through the decision framework, which allowed us to explore the consequences of diet mis-specification due to identification errors.

Dietary metrics.—For each scat, prey items were recorded and a percent volume of each prey item was visually estimated using a grid system (Doherty 2015). We were interested in the overall effect of predation on taxonomic and functional groups; thus, prey items were grouped into eight categories. Because we were interested in the potential impact to native CWR mammals, we segregated mammalian prey as native or non-native and grouped them according to mean adult size (Van Dyck and Strahan 2008), where medium-sized native mammals corresponded to the CWR range (35–5,500 g) and large and small native mammals were grouped above and below this range. Non-native mammalian prey consisted of camels (*Camelus dromedarius*), feral house cats, and European rabbits (*Oryctolagus cuniculus*). Because rabbits are a common prey among both dingoes and feral cats, we were interested in the extent to which this species was shared between the two predators. Hence, rabbits received their own category. On the other hand, both camels and feral cats were represented very rarely ($n = 1$ and $n = 7$, respectively) and only in dingo scats; thus, we did not include these two species in our dietary overlap analyses. We grouped nonmammalian prey according to phylum (arthropods) or class (reptiles and birds). Plant material was present in some scats and classified simply as vegetation.

For each predator species, we calculated two diet metrics: frequency of occurrence and percent volume of dietary category. Frequency of occurrence assigns dietary categories as either present or absent, but by allocating equal weight to the presence of small and large quantities of food items, tends to overestimate the importance of some foods (Weaver 1993). We removed trace amounts (i.e., < 5% total volume sensu Corbett 1989) from calculations to correct for the overrepresentation of food items that are consumed in small amounts (Klare et al. 2011). Percent volume is defined as the percentage volume of each prey item within each scat. This method tends to underestimate the importance of easily digestible food items; however, it is generally preferred when the goal of a study is to estimate the importance of different food categories (Klare et al. 2011).

We calculated the diversity (H) of prey items found in the scats of each species using the Brillouin diversity index (Brillouin 1956):

$$H = \frac{\ln N! - \sum \ln n_i!}{N}, \tag{1}$$

where N is the total number of individual prey categories recorded and n_i is the number of individual prey items found in the *i*th category. We plotted cumulative diversity (H_k) against the number of scats (k) after randomizing scat order, to determine whether the diets of dingoes and cats had been adequately sampled.

Dietary overlap (DO) between dingoes and cats was estimated using Pianka's index (Pianka and Pianka 1976):

$$DO_{cd} = \frac{\sum np_{ic}p_{id}}{\sqrt{\sum p_{ic}^2 \sum p_{id}^2}}, \tag{2}$$

where c and d represent the species (cats and dingoes, respectively) being compared, and p_i is the frequency of occurrence of

the *i*th prey category. Dietary overlap values range from 0 to 1, where 0 indicates no overlap and 1 indicates complete overlap. Although abundance-based methods of scat analysis are generally preferred for investigating dietary overlap (Klare et al. 2011), we use frequency of occurrence to be consistent with other studies. We present estimates of dietary overlap using percent volume in Supplementary Data SD1.

We conducted multivariate analyses using PCA on the percent volume of prey categories, to visually examine the extent of dietary overlap between the two species. Because vegetation is not considered an essential food item for either predator, we did not include it as a category in dietary overlap calculations or in the PCA. To evaluate the relative impact of dingoes and feral cats on CWR native mammals, we used a one-sided Fisher's exact test on the counts of scats with and without CWR native mammals present for each predator species.

Model evaluation.—To evaluate the effectiveness of this decision framework for resolving conflicted scat species origins, we calculated the dietary overlap between samples that were initially conflicted in their scat species identification (z) with samples that were initially nonconflicted (y). We characterized the diet of each predator provided that there was a sufficient sample size of conflicted scats, as determined from the cumulative diversity estimates. We then modified the index from equation 2 to calculate the overlap of the contents of samples z with samples y for predator x (either cats or dingoes):

$$DO_{zy}(x) = \frac{\sum np_{iz}p_{iy}}{\sqrt{\sum p_{iz}^2 \sum p_{iy}^2}}. \tag{3}$$

We performed a one-tailed permutation test ($\alpha = 0.05$—Mantel 1967), which compared the $DO_{zy}(x)$ value to the distribution generated from 1,000 permutations of this index where the scat sample was randomly reassigned as either originating from a conflicted (z) or nonconflicted (y) identification. If our framework has accurately assigned identifications to conflicted scats, we would expect $DO_{zy}(x)$ to be similar to or higher than the dietary overlap of randomly drawn scat samples. However, if the framework performed poorly, we would expect $DO_{zy}(x)$ to be significantly lower than the dietary overlap generated at random. Hence, an inability to reject the null hypothesis would indicate that our framework was effective in accurately resolving conflicted scat species identifications.

RESULTS

Expected dietary overlap ignoring uncertainty.—The extent of dietary overlap between dingoes and cats varied with the method used to identify scat species origin (Fig. 3). When only laboratory identifications were considered, the extent of dietary overlap was twice the extent of overlap when uncertainty in scat species origin was resolved through the decision framework (0.44 versus 0.22), and the *CI*s of these estimates did not overlap. When only field identifications were used, the estimates of dietary overlap were not significantly different from those obtained using the decision framework (0.24 versus 0.22). The PCA comparisons showed that when uncertainty in scat species origin was resolved, there was
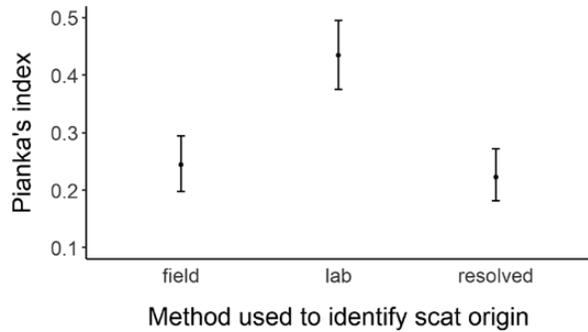
Fig. 3.—Extent of dietary overlap between dingoes and feral cats at Matuwa indigenous protected area (IPA), as measured by Pianka's index using frequency of occurrence data, relative to the method of scat donor species identification.

very little overlap between the diets of dingoes and cats (Fig. 4A). When only field identifications were used, this overlap increased only slightly (Fig. 4B), but when only laboratory identifications are used, this overlap grew considerably to encompass dietary groups previously indicated to have little overlap (e.g., reptiles, arthropods, CWR mammals; Fig. 4C).

Evaluation of decision framework to reduce errors in scat species identification.—There were 342 nonconflicted dingo scats, 277 nonconflicted feral cat scats, and 72 scats (10.3%) with conflicted identifications. When applying our decision framework for resolving scat species origin (Fig. 2), five scats had not been identified in the field and were hence discarded. Fourteen of the conflicted scat identifications had DNA available for testing and we were able to resolve the identifications for 11 using the DNA results. We resolved the identities of an additional 22 scats in the next step of the decision process by using the identification of the more certain observer to assign predator identity to the scat. Next, we calculated observer error rates of both definite and probable scat species identifications for each observer using the results of genetic analysis. The error rate for the field (9.1%, $n = 11$) was lower than the error rate for the laboratory (57.1%, $n = 14$) when both observers were certain. We used the field identification of scat species origin when the field certainty was definite, to resolve 38 scat identifications at this stage. Despite low sample sizes, it appeared that the error rates for both observers were likely very high when they were not certain of their identifications (80%, $n = 5$ for field; 60%, $n = 5$ for laboratory). It is for this reason that we chose to first resolve scat identifications by the more certain observer rather than simply relying on the observer with the lower error rate. Finally, one scat remained that could not be resolved because both observer certainty scores were classed as only probable; this scat was discarded because of the high observer error rates at this classification.

Of the 71 scats with conflicted identifications that were resolved through our decision framework, 11 were assigned as originating from dingoes and 60 from feral cats. Examination of the cumulative diversity of prey items from both predators (Fig. 5) indicates that these sample sizes are sufficient to characterize the diets of feral cats but not dingoes. Hence, to evaluate the decision framework, we examined the dietary overlap between initially conflicted and nonconflicted scats of feral cats only. This index revealed a very high agreement between these
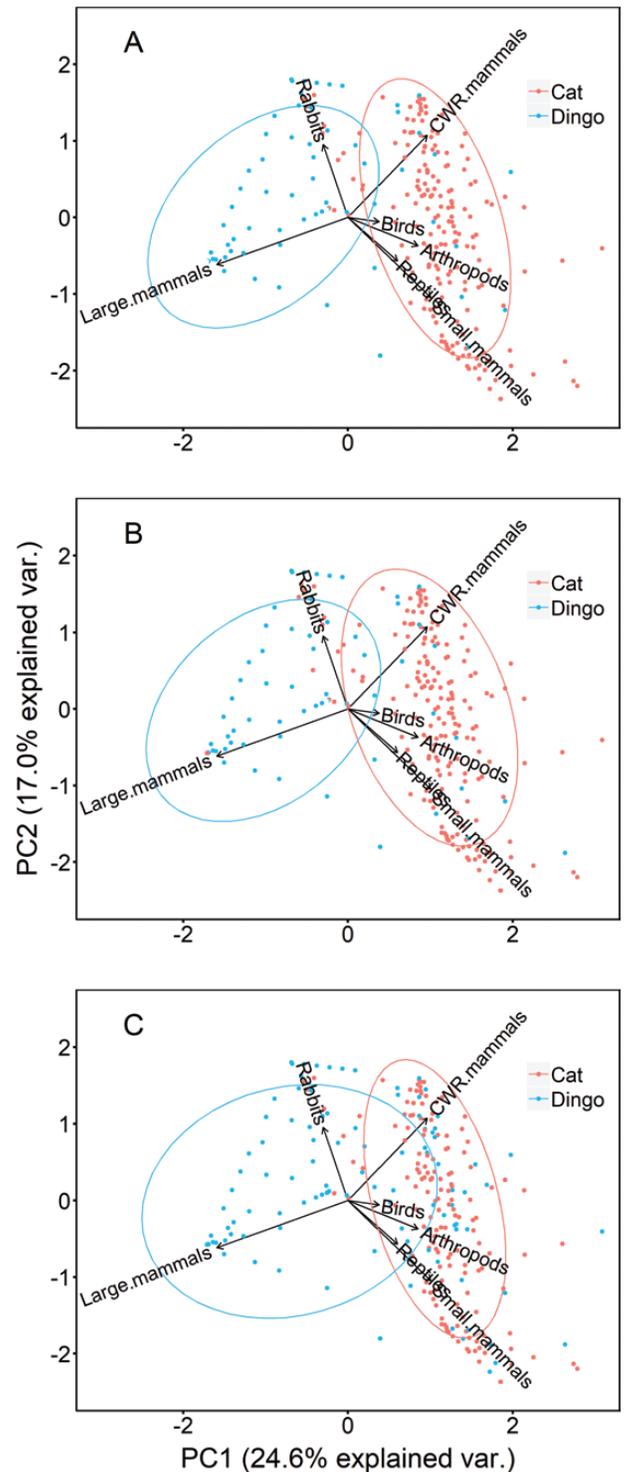

Fig. 4.—Principal component analyses of dingo and feral cat diets from 690 scats collected at Matuwa indigenous protected area (IPA). Extent of dietary similarity varies depending on how scat species origin was identified. In (A) scat identifications are resolved through the decision framework, in (B) field identifications are used, and in (C) laboratory identifications are used. PC = principal component.

two groups of cat scats (DO$_{zy}$(cats) = 0.989) and a nonsignificant one-tailed permutation test statistic ($P = 0.26$). This demonstrates that the diet of feral cats described by the 60 resolved cat scats was not significantly different from the diet described

by the initial 277 nonconflicted cat scats and provides support for the approach used to resolve the origin of uncertain scats.

Predator diet overlap.—Thirty-six different prey items were identified from all scats after applying the decision framework to reduce uncertainty in scat species origin (Table 2). Cumulative diversity H_k of prey items in the diets of both cats and dingoes reached an asymptote well below the total number of scats analyzed (Fig. 5), indicating that we were able to adequately describe the diets of both predators from the sample of scats collected. Mammals, regardless of size, were consumed most frequently and in the greatest volume for both predators. The main prey items consumed by dingoes included large native mammals (*Macropus* spp.) and rabbits, whereas for cats the main prey items included CWR native mammals, small native mammals, and birds (Fig. 6). In addition, we found evidence of intraguild predation, with 2% of dingo scats containing feral cat remains (Table 2). Evidence of cattle was not found in any dingo scats.

With scat species origin resolved, the dietary overlap between dingoes and feral cats was 0.22 (bootstrapped *CI*s 0.18–0.27), indicating a low level of dietary overlap between the two predators (Fig. 3). Critical weight range native mammals accounted for 44.0% of the diet by volume for feral cats compared to only 7.2% for dingoes; and occurred in 64.7% of the cat scats and 12.5% of the dingo scats. The occurrence of CWR mammals in the diets of the two predators was significantly higher for cats (Fisher's exact test: $P < 0.001$).

DISCUSSION

Scat analyses are a useful and common method by which interspecific competition of predators, and their potential relative impacts on prey, are examined (Hayward and Kerley 2008; Glen et al. 2011). However, because uncertainty in the identification of predator scats has the potential to obfuscate the extent of resource competition within a predator guild, we developed a decision framework to identify and then resolve potential errors in scat identifications. This framework (Fig. 2) relies on using multiple trained observers to identify scats that have the potential to be misidentified and then applies molecular identification techniques to a subset of these scats to
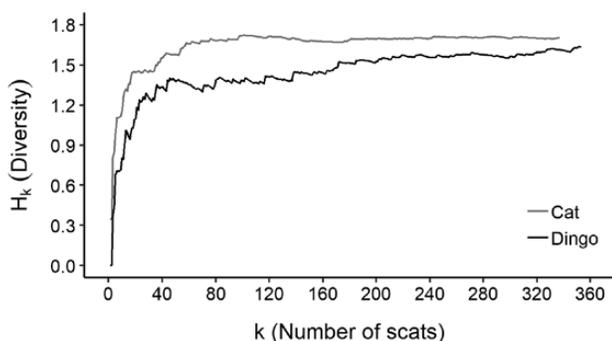

Fig. 5.—Cumulative dietary diversity as indicated by the Brillouin index (H_k) of dingo and feral cat prey items with increasing number of scat samples (*k*) at Matuwa indigenous protected area (IPA).

determine which observer is more accurate in identifying the true scat donor species. Using this framework, we identified 72 potentially misidentified scats (10.3% of total sample) and confidently assigned identifications to 71 (99%) of them.

To examine how error in the identification of predator scats can affect conclusions about the ecological interactions between predators, we examined the diets of an apex predator (dingo) and a mesopredator (feral cat) from field-collected scats that were identified by two separate trained observers, first in the field and then in the laboratory. We found that the dietary overlap of feral cats and dingoes based on field identification of scat species origin did not differ significantly from the dietary overlap when uncertainty was resolved (Fig. 3). However, when only laboratory identifications of scat species origin were used, the estimate of dietary overlap was twice as high as the estimate from when uncertainty was resolved through the decision framework (Fig. 3). Reliance on laboratory identifications of scat species origin would have likely led us to infer that dingoes and feral cats compete more strongly for prey than they likely do. In a management context, this inference might lead us to overestimate the importance of competition-driven dingo suppression of feral cats and underestimate the need to control feral cats via other means (Doherty et al. 2017).

By combining the use of trained observers and molecular genetic techniques to identify scat donor species through a structured decision framework, our study seeks to minimize the bias inherent in each method while maximizing accuracy and cost-efficiency. It has been widely acknowledged that reliance on trained observers alone may result in bias from misidentification (Table 1). However, bias in fecal DNA analysis may also occur as a result of extraction and amplification, field factors such as age of fecal sample, weather conditions, diet, and season (Ruiz-González et al. 2013). Hence, scats with low quantity or quality of DNA may not be successfully amplified or sequenced, leaving the identification of the scat donor species unknown (Taberlet et al. 1999) or predation of one predator on another could provide false positives (Ernest et al. 2000; Farrell et al. 2000). To our knowledge, the effect of bias in molecular genetic techniques on comparative diet studies of predators has not been widely examined and represents an important area for future investigation.

In evaluating the accuracy of our decision framework, we found no difference in the diet of feral cats when we characterized their diets with scats that were initially conflicted in their identification of scat donor species (i.e., scats where one observer thought the scat was from a dingo, but the scat was later resolved thorough our decision framework to be from a feral cat) and when we used scats in which observers had high certainty and no conflicted identifications (one-tailed permutation test statistic, $P = 0.26$). We believe this gives strong support for our decision framework and that it correctly identified scat donor species. Finally, because our method does not rely on genetic testing of all scats, it is a low-cost option that is likely valuable to natural resource practitioners with limited budgets (Prugh and Ritland 2005).

Table 2.—Percent frequency occurrence (FO) excluding trace amounts and percent volume (Vol) of food items in the scats of dingoes (*Canis lupus dingo*) and feral cats (*Felis catus*) at Matuwa indigenous protected area (IPA), Western Australia.

Food category (adult mean body weight in grams)	Dingo		Cat	
	n = 353		n = 337	
	FO	Vol	FO	Vol
Large native mammals (> 5,500)	68.0	60.2	1.5	1.2
Red kangaroo, *Macropus rufus* (66,000♂; 26,500♀)	15.6	13.9	0.0	0.0
Euro, *Macropus robustus* (35,000♂; 16,000♀)	37.1	35.0	0.9	0.9
Unidentified macropod	15.3	11.3	0.6	0.3
Critical weight range native mammals (35–5,500)	12.5	7.2	64.7	44.0
Short-beaked echidna, *Tachyglossus aculeatus* (4,500)	10.2	5.8	0.0	0.0
Greater bilby, *Macrotis lagotis* (1,750♂; 950♀)	0.0	0.0	2.7	2.0
Golden bandicoot, *Isoodon auratus* (485)	0.3	0.1	1.5	1.0
Brush-tailed mulgara, *Dasycercus blythi* (123♂; 78♀)	0.6	0.4	28.5	18.7
Spinifex hopping mouse, *Notomys alexis* (35)	1.7	0.9	46.0	22.3
Small mammals (< 35)	2.5	1.0	65.6	32.2
Bolam's mouse, *Pseudomys bolami* (16)	0.0	0.0	2.4	0.5
Desert mouse, *Pseudomys desertor* (25)	1.4	0.5	41.2	20.9
Sandy inland mouse, *Pseudomys hermannsburgensis* (12)	0.6	0.1	21.1	6.4
Unidentified rodent	0.0	0.0	9.5	0.9
Kultarr, *Antechinomys laniger* (30♂; 20♀)	0.3	0.2	2.4	0.8
Fat-tailed dunnart, *Sminthopsis crassicaudata* (15)	0.0	0.0	0.0	0.0
Lesser hairy-footed dunnart, *Sminthopsis youngsoni* (10.1)	0.3	0.1	3.3	0.9
Long-tailed dunnart, *Sminthopsis longicaudata* (18)	0.0	0.0	0.9	0.4
Stripe-faced dunnart, *Sminthopsis macroura* (20)	0.0	0.0	1.2	0.4
Ooldea dunnart, *Sminthopsis ooldea* (11)	0.0	0.0	0.9	0.3
Unidentified dunnart, *Sminthopsis* sp.	0.3	0.1	5.3	0.6
Unidentified dasyurid	0.0	0.0	0.6	0.1
Rabbit, *Oryctolagus cuniculus* (1,580)	20.4	16.4	5.0	3.5
Other mammals				
Camel, *Camelus dromedarius* (800,000)	0.3	0.3	0.0	0.0
Dog, *Canis* sp. (16,800)	0.3	0.1	0.0	0.0
Cat, *Felis catus* (4,225)	2.0	1.6	0.0	0.0
Bird	11.0	5.5	43.0	10.3
Non-emu birds	5.9	1.6	42.4	10.0
Emu, *Dromaius novaehollandiae*	5.1	3.9	0.6	0.3
Reptiles	2.5	1.2	26.4	3.9
Skink	0.6	0.1	18.1	1.9
Dragon	0.3	0.1	3.9	0.5
Varanidae	1.4	1.0	5.3	0.9
Snake	0.6	0.0	3.9	0.6
Arthropods	1.7	0.2	25.2	2.9
Beetle	0.0	0.0	3.3	0.2
Grasshopper	1.4	0.2	20.8	2.5
Scorpion	0.0	0.0	0.9	0.1
Centipede	0.3	0.1	0.6	0.1
Vegetation	9.3	6.4	7.1	1.7

Our framework was designed to identify and resolve potential errors in scat species identification by flagging differences in identifications between two trained observers. However, we acknowledge that two observers could assign the same scat donor species and both be incorrect (see Davison et al. 2002). Our framework did not specifically address this possibility because we did not think that there was a high probability of this occurring given that we only had two predators in the system and that the size difference between them was large. In the situation where there are more than two predators of similar sizes, our decision framework could be modified to rely on observer error rates rather than observer confidence scores to accurately classify scat origin. In this case, we suggest testing experts on a subset of scats whose origins have been identified through genetic testing to better characterize observer error rates (Morin et al. 2016).

Relative threats and dietary overlap.—With uncertainty in scat origin resolved through our decision framework, our estimate of dietary overlap for dingoes and feral cats was considerably lower (0.22) than has been reported for these two species in other studies (0.65—Paltridge 2002; 0.496—Glen et al. 2011; 0.45—Doherty 2015). In classical competition theory, two competing species can coexist when there is some degree of resource partitioning in diet, space, or time (Gause 1934). Spatial coexistence has been observed between predators with low dietary overlap, such as between Eurasian badgers (*Meles meles*) and Iberian lynxes in Spain (Fedriani et al. 1999) and jaguars (*Panthera onca*) and pumas (*Puma concolor*) in Venezuela (Scognamillo et al. 2003). At our study site, both dingoes and feral cats co-occur across similar habitats (Wysong 2016). Yet the low level of dietary overlap between the two predators suggests that competition between the two species may be low,
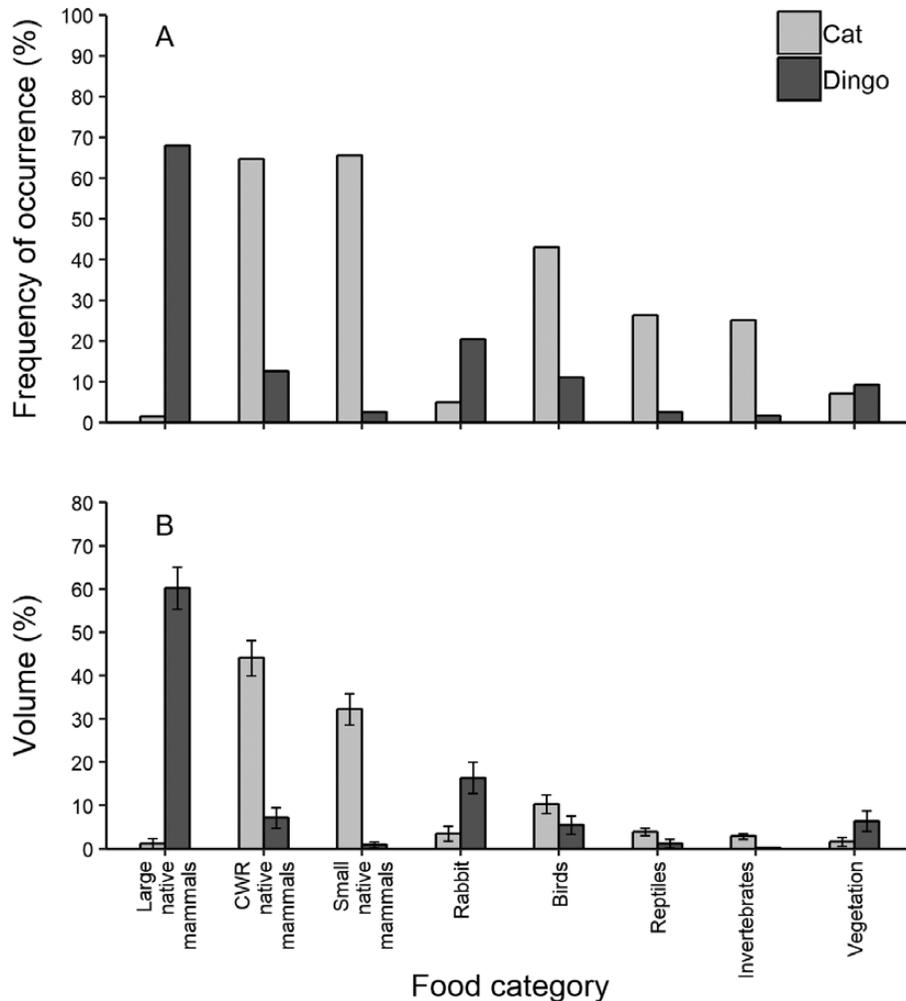
Fig. 6.—Comparison of the diets of dingoes and feral cats at Matuwa indigenous protected area (IPA), Western Australia shown in terms of (A) frequency of occurrence excluding trace amounts, and (B) percentage volume.

thus providing a mechanism for their coexistence, although prey availability, dietary overlap, and competition may vary with productivity, either annually or seasonally (Greenville et al. 2014). At the same time, the occasional occurrence of cat remains in the scats of dingoes documented in this study is consistent with other studies (Allen et al. 2015) and indicates the potential for interference competition between the two species. Dingoes are known to kill cats without eating them; in this case, interference derived from scats alone is likely an underestimate (Moseby et al. 2012). However, it is possible that these cats were scavenged rather than killed, and it is likely that feral cats can still co-occur with dingoes while avoiding them temporally (Brook et al. 2012) or at small spatial scales (Brook 2013).

Critical weight range mammals occurred five times more frequently in cat scats than in dingo scats (Fig. 6). Although this higher frequency of occurrence may not necessarily equate to a higher impact of feral cats at the population level as impact also depends on the density of feral cats relative to dingoes in the area, it does suggest that CWR mammals are at a higher relative risk from cats than from dingoes. However, it is important not to dismiss the potential impacts of dingoes on CWR mammals, which can vary regionally and temporally and may have

a greater impact on those species at the higher end of the CWR spectrum (Doherty et al. 2018). Of the five CWR mammals that occurred in the predators' scats, two occurred very infrequently (greater bilby [*Macrotis lagotis*] and golden bandicoot [*Isoodon auratus*]), most likely because they are very rare at the site (Dunlop and Morris 2009). Of the other three CWR mammals, two were on the lower end of the CWR spectrum and also occurred much more frequently in cat scats than in dingo scats (brush-tailed mulgara [*Dasycercus blythi*], 47.5 times greater in cat scats; spinifex hopping mouse [*Notomys alexis*], 27.1 times greater in cat scats). Hence, mammals at the lower end of the CWR spectrum may be much more heavily impacted by feral cats than those at the higher end of the range.

There is strong evidence that predation by cats is a significant factor in the decline of native mammals at the local level (Denny and Dickman 2010; Woinarski et al. 2014). The findings of this study are consistent with this evidence and suggest that dingoes at the study site do not pose as large a predation threat to CWR mammals as do cats. Apart from the short-beaked echidna (*Tachyglossus aculeatus*), which was recorded in ~10% of dingo scats, no other small or CWR native mammal was recorded in dingo scats with a frequency greater than 2%,

and most were either absent or occurred in less than 1% of scats (Table 2). The results of this study are in contrast to studies that have suggested that dingoes prefer to prey on small- and medium-sized mammals (Allen and Fleming 2012). Our study results are restricted to a 2-year period that excludes summer months. It is possible that dingoes could switch to small- and medium-sized prey should their preferred prey of macropodids become scarce, and we recommend further research on the link between prey diversity and availability and predator impacts (Greenville et al. 2014).

Management implications.—Our results highlight the importance of the feral cat as a global threat to biodiversity (Medina et al. 2011), and show that teasing apart the relative ecological function of this species compared with other sympatric predators will be crucial for effective and integrated management decisions (Doherty and Ritchie 2017). Around the globe, the feral cat now coexists with native predators such as island foxes (*Urocyon littoralis*) in the United States (Bridges et al. 2015), and various carnivores in Madagascar (Farris et al. 2015) and South America (Merino et al. 2009). In arid Australia, our results suggest that controlling feral cats is likely to provide the most direct benefit to mammals of conservation concern (i.e., native small and CWR mammals) as well as non-ratite birds. However, we caution that baiting for feral cats must consider potential nontarget impacts to dingoes, which are susceptible to baiting (Burrows et al. 2003) and have been known to take feral cat baits (Wysong 2016).

Control of dingoes is likely to directly benefit mostly large native prey such as the euro (*Macropus robustus*) and red kangaroo (*M. rufus*), as well as the non-native European rabbit, which is classified as a pest. Our results indicate that dingo control within environments and with predator–prey assemblages similar to our study site might have few or no conservation benefits; in our study area, the only native mammal potentially to benefit from dingo control is the short-beaked echidna (Table 2), which is widespread and not of conservation concern (Van Dyck and Strahan 2008). Dingoes may play an important role in controlling overgrazing by kangaroos and other non-native herbivores, hence maintaining vegetation structure and resources necessary for CWR mammals (Newsome et al. 2015). In this regard, dingo control may have negative consequences for the survival of CWR mammals. It should be noted here that another invasive mesopredator known to interact with both dingoes and cats (Greenville et al. 2014), the red fox, is largely absent from our study area, and without further overlap studies our results should not be extrapolated to locations where these three species co-occur.

The likely direct and indirect effects of predator control on both native and non-native prey are uncertain, and nonexperimental dietary analysis can only infer these effects. Our results imply that removing dingoes from the study site could result in release of an introduced herbivore, the European rabbit. This could have either positive or negative benefits to small- and medium-sized mammals depending on whether feral cats switch from a predilection for small- and medium-sized native mammals to rabbits or whether an increase in availability of rabbits and absence of dingoes leads to an increase in abundance of cats, creating additional predation pressure on small- and medium-sized mammals. To examine these effects, perturbation experiments would be ideally carried out (see Lurgi et al. 2018), but these may be prohibitively expensive and require many years to monitor and measure the outcomes. In the absence of direct experimentation and evidence supporting the case for lethal control, we caution that the negative indirect effects of dingo control on native CWR mammals might outweigh any possible short-term direct benefits, and therefore needs to be carefully considered in any pest and wildlife management actions.

SUPPLEMENTARY DATA

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

Supplementary Data SD1.—Dietary overlap estimates, measured by Pianka's index (PI) calculated from % volume of prey in scats, relative to the method of identification (MOI) of scat species origin with 95% bootstrapped *CI*s.

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