



# The (Non)Effects of Lethal Population Control on the Diet of Australian Dingoes

Benjamin L. Allen<sup>\*‡</sup>, Luke K.-P. Leung

School of Agriculture and Food Sciences, the University of Queensland, Gatton, Queensland, Australia

## Abstract

Top-predators contribute to ecosystem resilience, yet individuals or populations are often subject to lethal control to protect livestock, managed game or humans from predation. Such management actions sometimes attract concern that lethal control might affect top-predator function in ways ultimately detrimental to biodiversity conservation. The primary function of a predator is predation, which is often investigated by assessing their diet. We therefore use data on prey remains found in 4,298 Australian dingo scats systematically collected from three arid sites over a four year period to experimentally assess the effects of repeated broad-scale poison-baiting programs on dingo diet. Indices of dingo dietary diversity and similarity were either identical or near-identical in baited and adjacent unbaited treatment areas in each case, demonstrating no control-induced change to dingo diets. Associated studies on dingoes' movement behaviour and interactions with sympatric mesopredators were similarly unaffected by poison-baiting. These results indicate that mid-sized top-predators with flexible and generalist diets (such as dingoes) may be resilient to ongoing and moderate levels of population control without substantial alteration of their diets and other related aspects of their ecological function.

**Citation:** Allen BL, Leung LK-P (2014) The (Non)Effects of Lethal Population Control on the Diet of Australian Dingoes. PLoS ONE 9(9): e108251. doi:10.1371/journal.pone.0108251

**Editor:** Joseph K. Bump, Michigan Technological University, United States of America

**Received:** July 31, 2014; **Accepted:** August 25, 2014; **Published:** September 22, 2014

**Copyright:** © 2014 Allen, Leung. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

**Data Availability:** The authors confirm that all data underlying the findings are fully available without restriction. All relevant data are within the paper.

**Funding:** Funding for components of this study was provided by the Caring for Our Country and Natural Heritage Trust government funding programs. Some of this funding was administered by the South Australian Arid Lands Natural Resources Management Board. These funding bodies had no role in the design, implementation, analysis or publication of this study.

**Competing Interests:** Benjamin Lee Allen is an editorial board member for PLoS ONE. However, this does not alter our adherence to PLOS ONE Editorial policies and criteria.

\* Email: benjamin.allen@daff.qld.gov.au

‡ Current address: Robert Wicks Pest Animal Research Centre, Biosecurity Queensland, Toowoomba, Queensland, Australia

## Introduction

Terrestrial carnivores face energetic constraints that influence many aspects their breeding, feeding and social ecology [1,2]. Consequently, carnivores exhibit a wide variety of reproductive and hunting strategies to meet their energetic requirements. Smaller carnivores are often highly fecund, breeding continually throughout the year and adopting generalist diets primarily comprising of invertebrates and small mammals. Such carnivores might be typified by European badgers (*Meles meles*) or feral cats (*Felis catus*) (e.g. [3,4]). Larger carnivores often breed only once annually, produce fewer young and rely on a much more narrow range of large mammal prey. Polar bears (*Ursus maritimus*), lions (*Panthera leo*) and grey wolves (*Canis lupus*) exhibit these characteristics (e.g. [5,6]). The prey size preferred by carnivores scales positively with carnivore body mass, where a transition point from small to large prey preference occurs in carnivores weighing approximately 14–21 kg [1,7]. Mid-sized carnivores in this weight range often exhibit hunting strategies that can reflect aspects of either larger or smaller carnivores, which can be modulated by various social constraints. These consumptive and non-consumptive functional effects of carnivores can strongly influence the structure and resilience of food webs and indirectly enhance biodiversity conservation [8–10].

Cooperative group hunting facilitates the acquisition of sufficient prey or energy resources typically unattainable by

individuals foraging alone, and is a feature common to many large carnivores. For example, African wild dogs (*Lycaon pictus*) in larger groups prefer prey weighing 120–140 kg, whereas, those in smaller groups prefer prey of similar weight to themselves (16–32 kg; [11]). Lions also hunt in groups, preferring prey weighing 190–550 kg [5]. Large ungulates are primary prey for group-hunting grey wolves [6,12]. Individuals within such groups possess hunting skills that, when combined with those of their associates, allow the group to be successful in capturing and subduing the prey resources they individually require. This suggests that alterations to group composition (or demography) may affect hunting success, individual fitness and ultimately the persistence of the group or population and their ecological function [13,14]. The lethal control of carnivores (often undertaken for the protection of livestock, managed game or humans) is one way that alters the composition of carnivore populations [15]. Lethal control includes shooting, trapping or poisoning in different parts of the world, and can target problem individuals or entire populations across large areas. That the removal of individuals from group-hunting large carnivores can sometimes influence the sustainability of their populations is well known (e.g. [16,17]), but limited information exists on the effects of lethal control or social disruption on the diet or function of mid-sized carnivores with flexible and adaptable foraging abilities.

**Table 1.** Mean body weights of Australian dingoes from 17 wild populations.

Location	Mean body weight (kg)	N =	Reference
Kumbarilla Forest	13.0	7	[70,71]
Central Australia	13.5	50	[20]
Sturt Stony Desert	13.5	2	B. Allen, unpublished data
Tanami Desert	13.7	143	[72]
NE NSW forests	14.1	100	G. Ballard, unpublished data
Taunton National Park	14.6	9	[70,71]
Victorian highlands	15.1	28	[20]
Dunluce Station	15.8	5	[70,71]
Kosciuszko National Park	15.8	23	[73]
Blue Mountains	16.0	47	[74]
Kakadu National Park	16.3	19	[20]
Fraser Island	16.7	147	L. Behrendorff, unpublished data
Strzelecki Desert	16.8	17	[19,35]
Peri-urban areas of greater Brisbane	17.0	32	B. Allen, unpublished data
Charleville	17.7	6	[70,71]
Idalia National Park	18.0	4	[70,71]
Stratford	19.6	7	[70,71]
<b>TOTAL</b>	<b>15.7</b>	<b>646</b>	

doi:10.1371/journal.pone.0108251.t001

As a type of dog, dingoes (*Canis lupus dingo* and hybrids) are classic mesopredators [18], yet usurped their present top-predator status subsequent to their introduction to Australia about 5000 years ago, coincident with decline and extinction of the thylacine (*Thylacinus cynocephalus*) on the mainland. Dingoes typically weigh 12–17 kg (Table 1), require about 750 g/kg body weight in food per day with semi-frequent watering [19], and are the most closely related canid to grey wolves ([18,20]; but see also [21]). Dingoes breed once annually (with a birth peak in winter) and can exist individually or in groups of over 20 (usually 4–10; [19,22]).

Dingoes have flexible and generalist diets, and populations are known to persist on a variety of prey from invertebrates to water buffalo (*Bubalus bubalis*) (e.g [23,24]). Some populations sometimes use group hunting to capture relatively large kangaroos (*Macropus* spp.; Australia's largest native terrestrial mammals; females 18–40 kg, males 55–85 kg), while others live in groups yet forage individually on small mammals (<200 g) or European rabbits (*Oryctolagus cuniculus*; ~1.5 kg) [23,25,26]. The distribution of dingoes presently extends across ~85% of the continent and is naturally expanding back into the few remaining areas

**Table 2.** Short-term changes (mean days since baiting = 54) in dingo passive tracking index (PTI) values in response to 11 poison-baiting programs undertaken at the study sites between July 2008 and August 2011, showing the net baiting-induced reductions or increases in dingo activity (adapted from [29]).

Baiting program ID	Site	Post-control survey date	% PTI change in the baited area	% PTI change in the unbaited area	Net% change in PTI in the baited area
CD1	Cordillo Downs	22-Jul-09	93.8%	–21.1%	114.8%
CD2	Cordillo Downs	20-Jan-10	21.8%	89.4%	–67.6%
Q1	Quinyambie	08-Jul-08	44.4%	70.0%	–25.6%
Q2	Quinyambie	30-Sep-09	5.3%	–48.4%	53.7%
Q3	Quinyambie	29-Jun-11	67.7%	31.8%	35.8%
Q4	Quinyambie	03-Aug-11	59.9%	–56.8%	116.7%
T1	Todmorden	15-Jan-09	0.0%	–604.7%	604.7%
T2	Todmorden	27-Feb-09	–75.0%	–2650.0%	2575.0%
T3	Todmorden	22-Apr-09	50.2%	67.2%	–17.0%
T4	Todmorden	23-May-09	100.0%	90.7%	9.3%
T5	Todmorden	04-Feb-10	–100.0%	77.8%	–177.8%

Note: Positive values denote% reductions in dingo activity; negative values denote% increases in dingo activity. Reductions>100% indicate that dingoes present prior to baiting were removed, along with additional immigrating dingoes as well.

doi:10.1371/journal.pone.0108251.t002

**Table 3.** Total number of prey tracks (footprints) observed during 32 standardised surveys undertaken at the study sites during the study period (see [30] for details).

Site (N surveys)	Treatment	Birds	Rabbits	Small mammals <sup>^</sup>	Macropods	Pigs	Echidnas	Frogs	Hopping-mice	Reptiles*	Goannas ( <i>Varanus</i> spp.)
Quinyambie (14)	B	1026	922	1942	12	ND	1	0	6105	213	2
	UB	948	1234	1554	1	ND	1	3	8883	190	0
Cordillo Downs (7)	B	134	16	593	25	7	ND	0	356	136	3
	UB	459	53	980	20	0	ND	37	130	252	11
Todmorden (11)	B	496	221	1366	89	NP	ND	8	393	377	18
	UB	470	9	1333	108	NP	ND	0	272	173	15

ND = Present, but not detected; NP = Not present;

<sup>^</sup>All dasyurids and rodents except for hopping-mice (*Notomys* spp.).

\*All reptiles except *Varanus* spp., mostly agamidae and scincidae.  
doi:10.1371/journal.pone.0108251.t003

where they were formerly eradicated in the early 1900s [27]. The broad-scale distribution of 1080-poisoned baits (hereafter referred to as 'baiting') is common across much of Australia to protect commercial sheep (*Ovis aries*), goats (*Capra hircus*) and cattle (*Bos indicus*, *B. taurus* or their crosses) from dingo predation [28]. Due to rapid reinvasion, dingo abundance is typically resilient to contemporary baiting practices over time [28–30]. However, baiting has been predicted by some to alter dingo function independent of changes in dingo abundance, inclusive of changing their diet from a relatively narrow variety of large prey to a broader variety of small and often threatened prey (e.g. [31–33]).

In this study, we experimentally test this hypothesis by evaluating the effects of repeated broad-scale poison baiting programs on dietary similarity and diversity of Australian dingo populations. In doing so, we illustrate how a social and mid-sized top-predator can respond to the repeated removal of some individuals and the disruption of social groups. The aim of this study was to determine whether or not dietary diversity and similarity were different between dingo populations exposed to lethal control and those that were left intact. The simple and common approach we use to compare dingo diets in baited and unbaited areas should be readily applicable to a wide range of other carnivores of various body sizes.

## Materials and Methods

### Study sites and design

The study was conducted on three large and privately-owned beef cattle stations in the arid zone of northern South Australia (NSA). Quinyambie Station is located in the sandy Strzelecki Desert (−30.871887, 140.970354), has a mean annual rainfall (MAR) of ~160 mm, and is comprised of parallel sand dunes dominated by hopbush (*Dodonaea viscosa*), buckbush (*Salsola kali*), and a variety of grasses and burrs including kerosene grass (*Aristida* spp.) and copperburr (*Sclerolaena* spp.). Cordillo Downs Station is in the far northeast of South Australia around the Sturt Stony Desert (−26.706477, 140.625876), receives a MAR of ~167 mm, and incorporates both large, irregular sand dunes and extensive stony gibber plains. These contain beefwood (*Grevillea striata*) and spinifex (*Triodia* spp.) on the dunes, Mitchell grass (*Astrelba* spp.) on the plains, and red gum (*Eucalyptus camaldulensis*) and mineritchie (*Acacia cyperophylla*) in the drainage lines. Todmorden Station is located on the edge of the Pedirka Desert in the central-north of the state (−27.139073, 134.756423), has a MAR of ~180 mm, and is comprised of sandy deserts dominated by mulga (*Acacia aneura*) stands, with stony plain and drainage line vegetation similar to Cordillo Downs Station. Rainfall means were derived from long-term Bureau of Meteorology (www.bom.gov.au) data collected daily from nearby weather stations at Birdsville (since 1892), Frome Downs Station (since 1889), Hamilton Station (since 1884), Innamincka (since 1882), Macumba Station (since 1891) and Todmorden Station (since 1949). Information on South Australian floral species was obtained from Kutsche and Lay [34].

Each of the three stations were divided into paired dingo-baited and unbaited treatment areas (separated by a buffer zone >20 km at the closest point) as part of a larger manipulative experiment investigating the effects of dingo control on the ecology and management of dingoes and threatened fauna (e.g. [29,30]). Treatments were considered independent given that GPS tracking of 18 dingoes (from both baited and unbaited areas) showed that scat collection sites were separated by at least 1–2 dingo home ranges, with dingoes exhibiting high site fidelity in both treatments (mean daily travel distance = 14.0 km, range = 7.8–18.8 km/day;

N = 3340 dingo-days of monitoring data; from [19,35]). Baiting programs at the sites typically occurred twice each year in the baited areas (in autumn and spring), and results from associated studies indicated that dingo population abundance trends at our study sites were resilient to baiting given the typical and variable levels of population reductions and/or increases experienced (Table 2) and rapid reinvasion of baited areas [29,30]. In a regional context (see [36] for details), Todmorden is within the most intensively baited region in NSA, while Cordillo Downs is surrounded by a mosaic of baited and unbaited areas. Quinyambie is bordered by the dingo barrier fence which separates sheep grazing areas from cattle grazing areas [27,37], and apart from regular baiting which occurs in some parts of a 30 km buffer zone along the fence, the treatment areas are surrounded by unbaited areas. Additional history of lethal dingo control in NSA and further detail on additional outcomes of baiting at the study sites are available elsewhere (e.g. [23,29,30,35,36,38]).

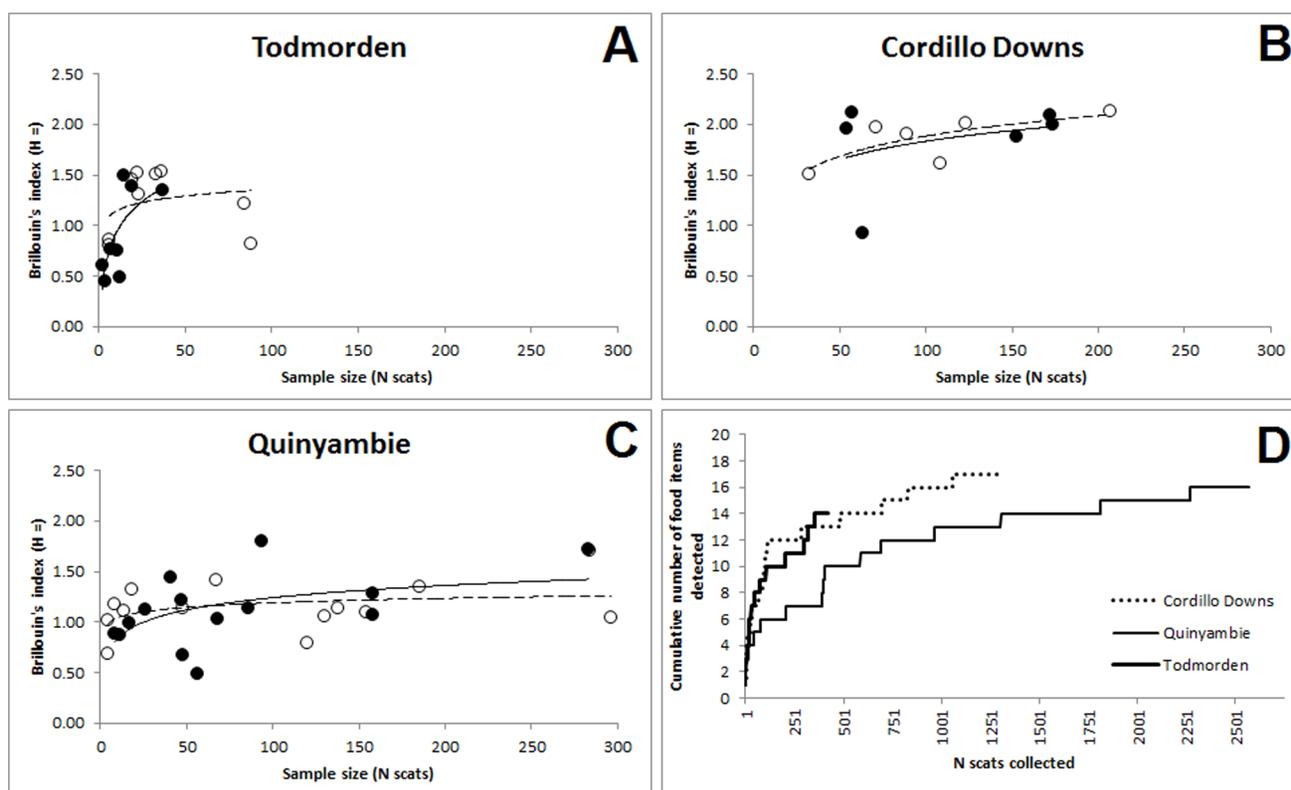
Although a variety of prey were present at each site, the relative abundance and availability of each prey species was not consistent between sites and varied throughout the study period in order to provide *in situ* assessments of changes in dingo diets in places with predominately small-, large- or mixed-sized prey. Thus, fauna assemblages were different between the three sites but similar between treatments at each site (Table 3; see also [30]), which were located on the same property. Most of the mammalian prey species identified in dingo scats from a given site were also present at each other site [23]. However, feral pigs (*Sus scrofa*) were found only on Cordillo Downs [39] and some small mammals identified in dingo scats have restricted distributions [40] and are likely rare or absent at some sites [41]. Kangaroos are uncommon at

Quinyambie, relatively common at Cordillo Downs and abundant at Todmorden ([42–44]; but see [30]). Rabbits are abundant at Quinyambie and uncommon at the other sites. Further information on the distribution of native and introduced prey species can be found elsewhere (e.g. [39,40,45,46]).

### Dingo scat collection and analysis

Dingo scats were collected from within each treatment area during repeated visits to the sites between May 2008 and May 2012. Dingo scats were distinguished from those of other predators (such as feral cats and red foxes, *Vulpes vulpes*) based on their size, shape, smell and placement [47]. Scat collection occurred six times at Cordillo Downs, nine times at Todmorden and 14 times at Quinyambie during this period. Because of the high abundance (and thousands of available scats) of dingoes at Quinyambie [19,36], scat collection was restricted to discrete, fenced (to exclude cattle) areas around five permanent artificial livestock watering points (two in unbaited areas, three in baited areas). At the other two sites, scats were collected from a wide variety of waterpoints, vehicle tracks, dry creek crossings, intersections and other focal locations where dingoes were expected to defecate more frequently. The same locations within each treatment were surveyed for scats at each repeated visit to each site. Thus, there was unequal sampling effort between treatments and sites, but there was equal sampling effort within treatments between surveys at each site [38].

Dingo scats collected were first sterilised and washed by a professional service provider who then searched each scat for the remains of prey fauna and other food items. Mammal species were



**Figure 1. The relationship between Brillouin's index and sample size at (A) Todmorden, (B) Cordillo Downs and (C) Quinyambie, and the relationship between the number of dingo scat samples collected and the number of prey or food items detected in scats from each of these three sites in northern South Australia.**

doi:10.1371/journal.pone.0108251.g001

**Table 4.** Sample sizes and Pianka's Index ( $O =$ ) values for dingo scats collected in baited and unbaited treatment areas during 29 surveys at three sites in northern South Australia, May 2008 to May 2012.

Study site	Survey Date	N scats			Pianka's Index
		Baited	Unbaited	Total	
Cordillo Downs	Oct-08	63	32	95	0.68
	Apr-09	54	89	143	0.98
	Jul-09	172	123	295	0.93
	Nov-09	174	207	381	0.91
	Jan-10	57	71	128	0.95
	Nov-10	153	108	261	0.89
	<i>Overall</i>	<i>673</i>	<i>630</i>	<i>1303</i>	<i>0.99</i>
Quinyambie	May-08	56	130	186	0.98
	Sep-08	48	154	202	0.99
	Mar-09	158	185	343	1.00
	Jun-09	158	296	454	0.99
	Sep-09	68	120	188	0.99
	Dec-09	283	138	421	0.99
	Jun-10	94	284	378	0.98
	Sep-10	41	48	89	1.00
	Apr-11	47	4	51	0.66
	Jun-11	11	8	19	0.68
	Jul-11	26	4	30	0.91
	Aug-11	8	14	22	0.96
	Feb-12	86	67	153	0.83
	May-12	17	18	35	0.78
<i>Overall</i>	<i>1101</i>	<i>1470</i>	<i>2571</i>	<i>1.00</i>	
Todmorden	Oct-08	11	6	17	0.95
	Jan-09	2	36	38	0.57
	May-09	37	84	121	0.98
	Aug-09	12	88	100	0.99
	Dec-09	0	33	33	N/A
	Feb-10	7	22	29	0.88
	Apr-10	4	6	10	0.76
	Sep-10	15	23	38	0.55
	Nov-10	19	19	38	0.89
	<i>Overall</i>	<i>107</i>	<i>317</i>	<i>424</i>	<i>0.96</i>

doi:10.1371/journal.pone.0108251.t004

identified from diagnostic characteristics of their hair (described in [48]). Results were reported at the genus level (or higher) where there was ambiguity over positive species-level identification. Non-mammal food items were categorised simply as birds, reptiles (inclusive of both smooth- and rough-scaled species, such as agamidae or scincidae), invertebrates or vegetation; these were only described to the species level opportunistically (by staff at the South Australian museum) according to the incidental presence of diagnostic bones and other features in the scat (such as teeth or scales). Results are expressed as the 'percent occurrence in scats' because many of the species detected in scats were relatively rare or uncommon [49]. Associated data on spatiotemporal variation in scat collection rates and the overall diet of dingoes at the sites are available in Allen [38] and Allen and Leung [23].

We made no attempt to compare or contrast dingo diets between sites, but were primarily concerned with dingo dietary

diversity and similarity between treatments within a given site. Therefore, we used Brillouin's Index to quantify and compare the *diversity* of dingo diets between baited and unbaited areas at each site according to the equation:

$$H = (\ln N! - \sum \ln n_i!)/N$$

where  $H$  = diversity,  $N$  = total number of individual prey recorded and  $n_i$  = number of individual prey items in the  $i$ th category [50]. Resulting  $H$  values typically range between 0 and 4.5, representing low and high dietary diversity, respectively. Similar values between treatments would indicate a similar range or suite of food and prey items is consumed by populations of dingoes in both baited and unbaited areas.

**Table 5.** The number (and proportion) of various food items found in 4,298 dingo scats collected from baited and unbaited treatment areas at three sites in northern South Australia, May 2008 to May 2012.

Food item	Cordillo Downs	Cordillo Downs	Quinyambie	Quinyambie	Todmorden	Todmorden
	Baited	Unbaited	Baited	Unbaited	Baited	Unbaited
<b>N=</b>	<b>673</b>	<b>630</b>	<b>1101</b>	<b>1470</b>	<b>107</b>	<b>317</b>
<i>Bos taurus</i>	155 (0.23)	156 (0.25)	80 (0.07)	82 (0.06)	31 (0.29)	133 (0.42)
<i>C. l. dingo</i> (prey)	7 (0.01)	1 (0.00)	6 (0.01)	12 (0.01)	1 (0.01)	2 (0.01)
<i>Felis catus</i>	4 (0.01)	1 (0.00)	1 (0.00)	4 (0.00)	0 (0.00)	1 (0.00)
<i>Macropus robustus</i>	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	2 (0.01)
<i>Macropus rufus</i>	28 (0.04)	22 (0.03)	39 (0.04)	4 (0.00)	39 (0.36)	111 (0.35)
<i>Nyctophilus geoffroyi</i>	0 (0.00)	0 (0.00)	1 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)
<i>Mus musculus</i>	110 (0.16)	89 (0.14)	13 (0.01)	39 (0.03)	3 (0.03)	9 (0.03)
<i>Notomys</i> spp.	30 (0.04)	44 (0.07)	98 (0.09)	187 (0.13)	5 (0.05)	11 (0.03)
<i>Oryctolagus cuniculus</i>	143 (0.21)	130 (0.21)	811 (0.74)	1103 (0.75)	16 (0.15)	19 (0.06)
<i>Pseudomys hermannsburgensis</i>	0 (0.00)	1 (0.00)	1 (0.00)	1 (0.00)	0 (0.00)	0 (0.00)
<i>Pseudomys australis</i>	0 (0.00)	0 (0.00)	0 (0.00)	1 (0.00)	0 (0.00)	0 (0.00)
<i>Leggadina forresti</i>	0 (0.00)	1 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)
<i>Rattus</i> spp.	118 (0.18)	65 (0.10)	7 (0.01)	43 (0.03)	0 (0.00)	0 (0.00)
<i>Sminthopsis crassicaudata</i>	0 (0.00)	1 (0.00)	2 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)
<i>Sminthopsis macroura</i>	49 (0.07)	93 (0.15)	14 (0.01)	10 (0.01)	0 (0.00)	1 (0.00)
<i>Sus scrofa</i>	3 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)
<i>Tachyglossus aculeatus</i>	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	2 (0.02)	0 (0.00)
Invertebrates	51 (0.08)	121 (0.19)	199 (0.18)	133 (0.09)	6 (0.06)	23 (0.07)
Vegetation	133 (0.20)	175 (0.28)	183 (0.17)	232 (0.16)	21 (0.20)	54 (0.17)
Birds	30 (0.04)	31 (0.05)	53 (0.05)	59 (0.04)	2 (0.02)	13 (0.04)
Reptiles	47 (0.07)	75 (0.12)	64 (0.06)	38 (0.03)	1 (0.01)	27 (0.09)

doi:10.1371/journal.pone.0108251.t005

We also used Pianka's Index to quantify and compare the *similarity* between dingo diets in baited and unbaited areas at each site for each individual survey and overall (all surveys pooled) using the equation:

$$O_{jk} = \left( \sum p_{ij} p_{ik} \right) / \left( \sum p_{ij}^2 \sum p_{ik}^2 \right)^{0.5}$$

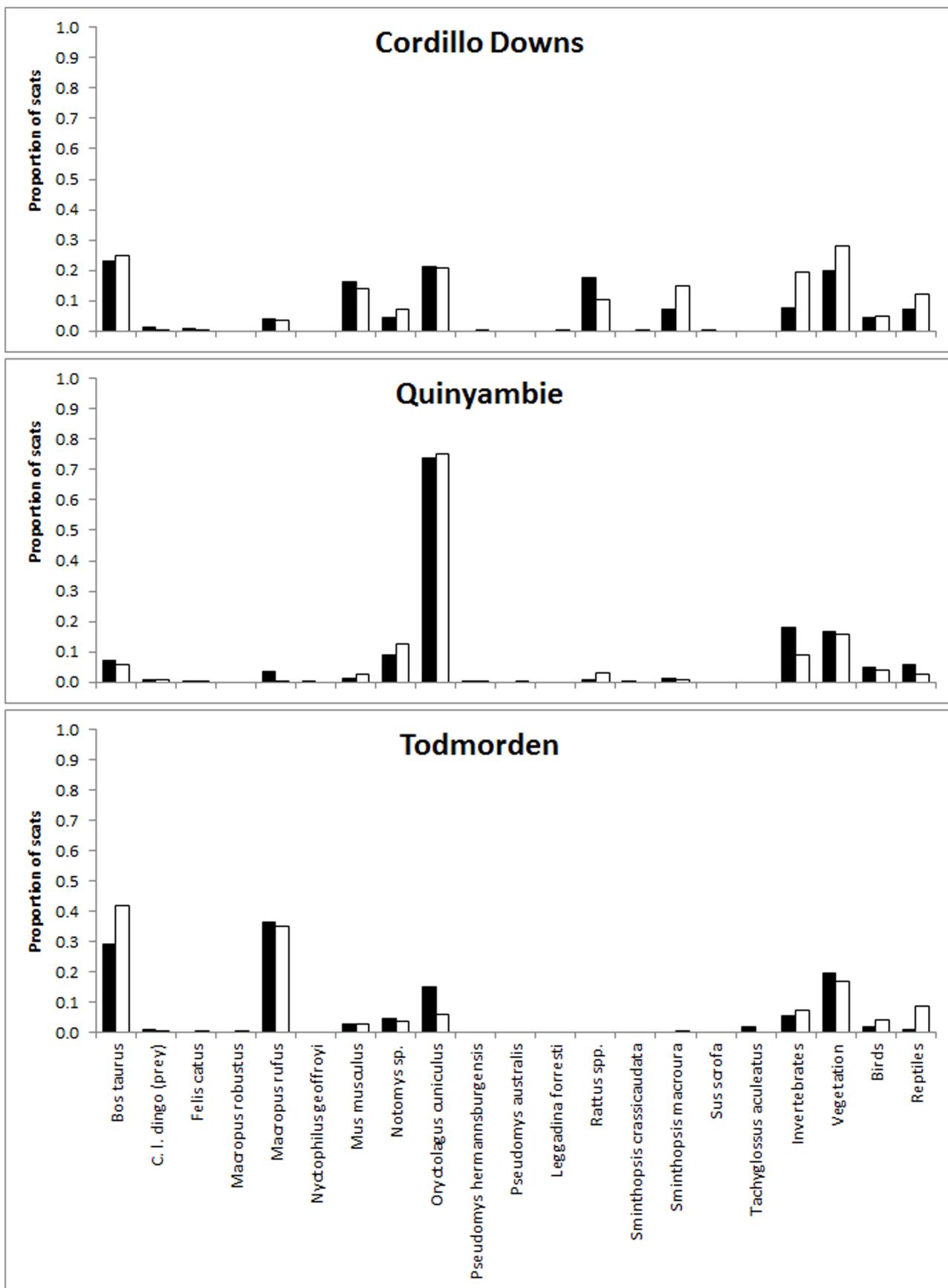
where  $O$  is the index of similarity or overlap,  $j$  and  $k$  are the dingo populations being compared (i.e. those in baited and unbaited areas), and  $P_i$  is the frequency of occurrence of the  $i$ th prey or food type [51]. Using this technique,  $O$  values range between 0 and 1, where values of 0 indicate complete dissimilarity (i.e. no prey in common) and values of 1 indicate complete similarity (i.e. diets are identical). Generalized linear regression was used to assess whether or not diet similarity (the response variable) changed through time (the predictor variable). We considered using additional techniques to further explore dietary differences (such as those described in [52]), but given our results (see below) and the aims of our study (see above), we considered them to be unnecessary and/or inappropriate for our data. The two simple but robust techniques we use have been widely used by others to compare the diets of dingoes with those of other sympatric predators, where dietary overlap between sympatric predators typically ranges between  $O = 0.5$ – $0.8$  (e.g. [53–59]);  $O$  values exceeding 0.75 have been described as substantial, strong or significant dietary overlap in these studies.

All procedures were carried out under permit issued by the South Australian Department of Environment and Heritage's Wildlife Ethics Committee (WEC 16/2008).

## Results

Baiting killed extant dingoes and temporarily reduced their population sizes at each site from time to time (Table 2), but baiting did not eliminate dingo populations, change the way dingoes interacted with sympatric predators, or change dingo movement behaviour and detectability [29,35,36]. We collected and analyzed 4,298 dingo scats – the second largest dingo diet study ever conducted [23,38]. Analyses of the relationship between Brillouin's index values and sample size indicated that approximately 50 scats were required to reliably compare and contrast dingo diets at our sites (Fig. 1). A total of 1,881 scats were collected in baited areas and 2,417 in unbaited areas (Table 4). Between 107 and 1,470 scats were collected in a given treatment and site. Thus, our sample sizes were sufficient for our analyses. Previous studies of dingo diet have similarly determined that approximately 30 scats are required to reliably compare and contrast dingo diets at other sites (e.g. [58]).

Between 14 and 17 different prey species or food items were detected in dingo scats at each site (Table 5, Fig. 1). The main prey consumed by dingoes were cattle, kangaroos, rabbits and a variety of small mammals, primarily dusky hopping-mice (*Notomys fuscus*), house mice (*Mus musculus*), stripe-faced dunnarts (*Sminthopsis macroura*) and long-haired rats (*Rattus villosissimus*)

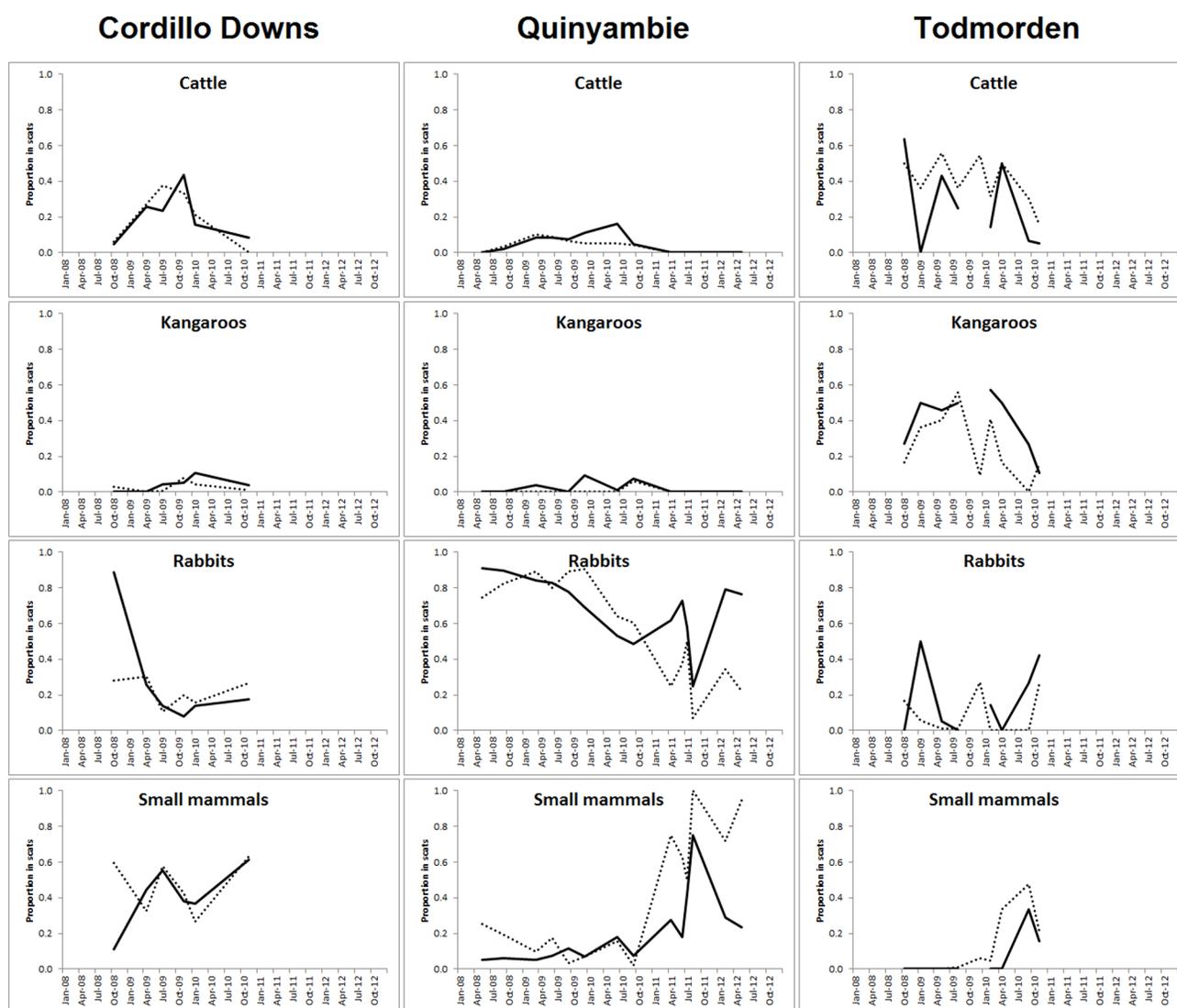


**Figure 2. Proportion of prey and food items detected in dingo scats from baited (solid bars) and unbaited (hollow bars) treatment areas at three sites in northern South Australia, May 2008 to May 2012.**  
doi:10.1371/journal.pone.0108251.g002

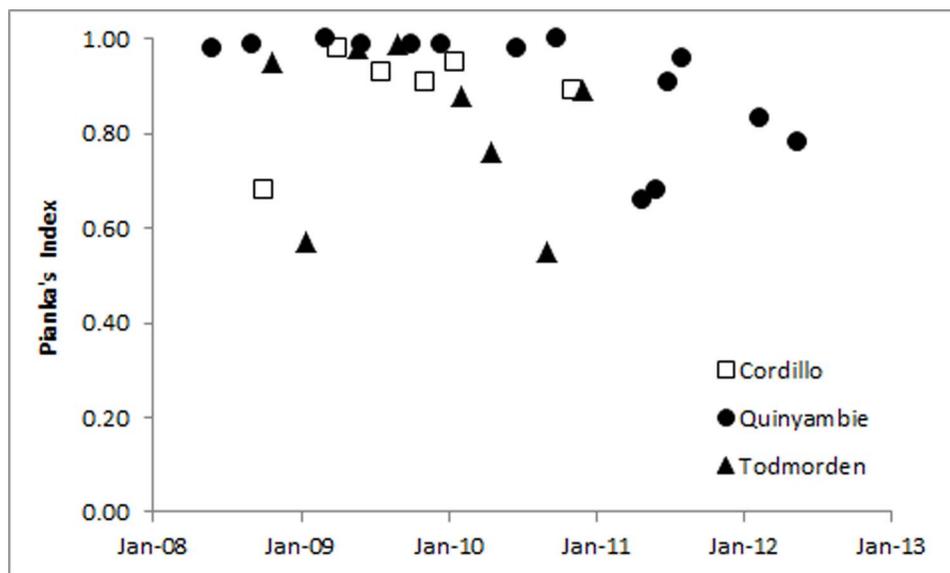
(Fig. 2; see also [23]). Vegetation and invertebrates also occurred relatively commonly in dingo diets. Temporal trends in the proportion of each of the main prey species in dingo scats were similar between treatments (Fig. 3). Brillouin's index ( $H$ ) values for Cordillo Downs (baited = 2.24, unbaited = 2.25), Quinyambie (baited = 1.64, unbaited = 1.54) and Todmorden (baited = 1.70, unbaited = 1.79) indicated a near-identical diversity or suite of food items were consumed by dingoes between treatments at each site, with a greater diversity of items at Cordillo Downs than at the other two sites.

Overall Pianka's index values for Cordillo Downs ( $O = 0.99$ ), Quinyambie ( $O = 1.00$ ) and Todmorden ( $O = 0.96$ ) likewise indicated that dingo diets in baited and unbaited areas were identical or near-identical at each site. Moreover, diets of dingoes in baited and unbaited areas were near-identical for most

individual surveys at each site as well (Table 4). Dietary similarity did not change through time for Cordillo Downs ( $r = 0.4590$ ,  $df = 5$ ,  $p = 0.3598$ ) or Todmorden ( $r = -0.2115$ ,  $df = 7$ ,  $p = 0.6151$ ). At Quinyambie, dingo diets were identical or near-identical for over two years subsequent to the commencement of baiting ( $r = 0.2402$ ,  $df = 7$ ,  $p = 0.5667$ ). Dietary similarity between treatments at Quinyambie appeared to decline in the latter half (years 3 and 4) of the study in 2011 and 2012 ( $r = -0.6474$ ,  $df = 13$ ,  $p = 0.0123$ ; Fig. 4) subsequent to the landscape-changing effects of the substantial rainfall events which occurred during this period [60]. Importantly however, for all sites and for the survey by survey analysis only (i.e. Fig. 4), Pianka's index values where  $O < 0.85$  were typically associated with sample sizes too low for a meaningful comparison of similarity between treatments (Table 4).



**Figure 3. Trends in the proportion of cattle, kangaroo, rabbit and small mammal remains found in dingo scats in baited (solid lines) and unbaited (broken lines) treatment areas on Cordillo Downs (left), Quinyambie (centre) and Todmorden (right) in northern South Australia.**  
doi:10.1371/journal.pone.0108251.g003



**Figure 4. Temporal variation in dingo dietary similarity ( $O=$ ) between baited and unbaited treatment areas at three sites in northern South Australia, May 2008 to May 2012.**

doi:10.1371/journal.pone.0108251.g004

## Discussion

Our results demonstrate that lethal dingo control did not alter dingo dietary diversity or similarity at our study sites. Brillouin's index values showed that the diversity of prey consumed by dingoes was near-identical between baited and unbaited areas at each site, indicating that dingoes in baited areas selected neither a wider nor narrower range of prey than dingoes in unbaited areas. Pianka's index values showed that the overall proportion of various prey consumed by dingoes was also either identical or near-identical between baited and unbaited areas; a trend reflected in results for individual surveys as well (Table 4; Fig. 4). This indicates that dingoes in baited and unbaited areas consumed the same proportion of various prey independent of the diversity or suite of prey species available (Table 5, Fig. 2). That temporal trends in the proportion of scats containing primary dingo prey were also similar between baited and unbaited areas further shows that prey consumption by dingoes is independent of dingo control (Fig. 3). These findings were consistent between sites dominated by the availability of large prey (Todmorden), small prey (Quinyambie) or mixed-sized prey (Cordillo Downs), suggesting that these results may be common across different ecosystems with different mammal assemblages.

Corbett and Newsome [25] showed that prey selection by dingoes varies according to the availability of different sizes of prey (from rodents to cattle), where dingoes typically prefer small mammals but consume an increasing proportion of larger mammals as smaller ones become unavailable. Newsome and colleagues [52,61] later showed that provision of anthropogenic food subsidies (such as livestock and rubbish) can disrupt this pattern, providing an essentially stable or year-round supply of food, which can lead to increased risk of hyperpredation to some threatened prey species (see also [23]). Additional information addressing optimal foraging theory and prey switching indicates that dingoes can easily and rapidly switch between prey of different types (i.e. mammals, birds, invertebrates) or sizes (e.g. [15,20,24,26,62]), consistent with the energetic studies of carnivores more generally [1,7]. Lone dingoes are also capable of

capturing and subduing adult kangaroos if necessary [26,63]. These findings suggest that although dingoes can and do switch between various prey types and sizes, perturbations to dingoes' social structure (such as the loss of individuals through baiting) may not automatically cause population-level changes in dingo diets. If dingoes in baited areas switched to prey different to those used by dingoes in nearby unbaited areas as a result of baiting, Pianka's index values should have been different between treatment areas or decreased over time, but such did not occur (Table 4, Fig. 4). If dingoes in baited areas utilized a wider or narrower range of prey than dingoes in nearby unbaited areas as a result of baiting, Brillouin's index values should have been markedly different, but such did not occur either (Fig. 2).

Although lethal control temporarily reduces dingo abundances (Table 2) and undoubtedly alters their social structures to some degree through poisoning or removal of some individuals [29,38,60], baiting did not appear to alter population-level dingo diets at our sites. These findings increase our understanding of the potential effects of lethal control on the behaviour and function of social mid-sized carnivores. Flexible social structures and generalist diets likely increase the resilience of such species to fluctuations in resource availability and biotic and abiotic perturbations that might normally be problematic for obligate group-hunting carnivores. Such characteristics likely contribute to the invasion success and global resilience of dingoes, coyotes (*Canis latrans*), red foxes and some other mid-sized carnivores (see [64] for details).

Some have called for cessation of lethal dingo control, claiming that such management approaches negatively affect dingo abundance and function and initiate trophic cascades that lead to biodiversity declines [9,31,65,66]. However, the experimental and empirical results of this study (and many others) do not support such claims. That the national distribution and density of dingoes is naturally increasing despite attempts at broad-scale lethal control [27] suggests that dingo function is not altered by baiting in ways that curtail dingo population growth. That dingo pack structure and social stability is resilient to moderate levels of lethal control [67] suggests that population growth rates are not

inhibited by the ongoing removal of some individuals (see also [68]). That dingo movement behaviour and detectability is not always altered by lethal control [35] suggests that dingo function is not altered in ways that might affect their study or their per capita contact rates with sympatric predator or prey species. That dingoes' numerical relationships with other sympatric predators are not altered by lethal control over time [29] suggests that dingo abundance or function is not altered in ways that might increase densities of other predators in extant food webs. That sympatric prey population trends fluctuate independent of dingo control [30] suggests that threatened fauna populations are not harmed by contemporary dingo control practices. That dingoes do not alter their diets in response to lethal control (this study) concurs with each of these previous findings, and further suggests that predation of particular prey types or species is not exacerbated by lethal control, but is rather a function of dingo density and prey/food availability and preference [23,52,69].

We conclude that while some large top-predators are clearly reliant on intact or robust group numbers or social structures to secure sufficient prey resources (such as lions, grey wolves or African wild dogs), mid-sized top-predators with flexible and generalist diets (such as dingoes) may be functionally and

numerically resilient to repeated moderate levels of population reduction over time in many cases. Where threatened fauna are expected to be influenced by managed predator populations, future studies might investigate the responses of threatened prey populations to lethal predator control (such as [30]) to confirm the potential effects of predator control on lower trophic levels.

## Acknowledgments

We're grateful to all those who helped collect the many dingo scats used in this study in spite of the heat, flies, burrs, sand and smell – your assistance was gratefully appreciated. Access to study sites was obtained from Greg Campbell and Greg Conners (Quinyambie), Janet and Anthony Brook (Cordillo Downs) and Douglas Lillcraip (Todmorden). Identification of prey remains in dingo scats was undertaken by Barbara Triggs. Helpful advice on analyses and comments on earlier drafts were provided by Al Glen, Guy Ballard, Joe Scanlan, Matt Gentle and Tom Newsome. The production of this report was undertaken as part of work supported by the Invasive Animals Cooperative Research Centre.

## Author Contributions

Conceived and designed the experiments: BA LL. Performed the experiments: BA. Analyzed the data: BA. Wrote the paper: BA LL.

## References

- Carbone C, Mace GM, Roberts SC, Macdonald DW (1999) Energetic constraints on the diet of terrestrial carnivores. *Nature* 402: 286–288.
- Gittleman JL, Harvey PH (1982) Carnivore home-range size, metabolic needs and ecology. *Behavioural Ecology and Sociobiology* 10: 57–63.
- Denny EA, Dickman CR (2010) Review of cat ecology and management strategies in Australia. Canberra: Invasive Animals Cooperative Research Centre.
- Kruuk H (1989) *The social badger*. Oxford: Oxford University Press.
- Hayward MW, Kerley GIH (2005) Prey preferences of the lion (*Panthera leo*). *Journal of Zoology* 267: 309–322.
- Mech LD (1970) *The wolf: the ecology and behaviour of an endangered species*. Garden City, New York: The Natural History Press.
- Carbone C, Teacher A, Rowcliffe JM (2007) The costs of carnivory. *PLoS Biology* 5: 0363–0368.
- Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, et al. (2011) Trophic downgrading of planet earth. *Science* 333: 301–306.
- Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, et al. (2014) Status and ecological effects of the world's largest carnivores. *Science* 343: 151–163.
- Brown JS, Laundre JW, Gurung M (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* 80: 385–399.
- Hayward MW, O'Brien J, Hofmeyr M, Kerley GIH (2006) Prey preferences of the African wild dog *Lycan pictus* (Canidae:carnivora): ecological requirements for conservation. *Journal of Mammalogy* 87: 1122–1131.
- Hayes RD, Farnell R, Ward RMP, Carey J, Dehn M, et al. (2003) Experimental reduction of wolves in the Yukon: ungulate responses and management implications. *Wildlife Monographs* 152: 1–35.
- Ordiz A, Bischof R, Swenson JE (2013) Saving large carnivores, but losing the apex predator? *Biological Conservation* 168: 128–133.
- Haber GC (1996) Biological, conservation, and ethical implications of exploiting and controlling wolves. *Conservation Biology* 10: 1068–1081.
- Allen LR (2013) *The impact of wild dog predation and wild dog control on beef cattle: large-scale manipulative experiments examining the impact of and response to lethal control*. Saarbrücken, Germany: LAP Lambert Academic Publishing.
- Winterbach HEK, Winterbach CW, Somers MJ, Hayward MW (2013) Key factors and related principles in the conservation of large African carnivores. *Mammal Review* 43: 89–110.
- Mech LD (2010) Considerations for developing wolf harvesting regulations in the contiguous United States. *Journal of Wildlife Management* 74: 1421–1424.
- Fleming PJS, Allen BL, Ballard G (2012) Seven considerations about dingoes as biodiversity engineers: the socioecological niches of dogs in Australia. *Australian Mammalogy* 34: 119–131.
- Allen BL (2012) Do desert dingoes drink daily? Visitation rates at remote waterpoints in the Strzelecki Desert. *Australian Mammalogy* 34: 251–256.
- Corbett LK (2001) *The dingo in Australia and Asia*. Marlestone: J.B. Books, South Australia.
- Freedman AH, Gronau I, Schweizer RM, Ortega-Del Vecchyo D, Han E, et al. (2014) Genome sequencing highlights the dynamic early history of dogs. *PLoS Genetics* 10: e1004016.
- Newsome TM, Ballard G, Dickman CR, Fleming PJS, van de Ven R (2013) Home range, activity and sociality of a top predator, the dingo: a test of the Resource Dispersion Hypothesis. *Ecography* 36: 914–925.
- Allen BL, Leung LK-P (2012) Assessing predation risk to threatened fauna from their prevalence in predator scats: dingoes and rodents in arid Australia. *PLoS ONE* 7: e36426.
- Corbett L (1995) Does dingo predation or buffalo competition regulate feral pig populations in the Australian wet-dry tropics? An experimental study. *Wildlife Research* 22: 65–74.
- Corbett L, Newsome AE (1987) The feeding ecology of the dingo. III. Dietary relationships with widely fluctuating prey populations in arid Australia: an hypothesis of alternation of predation. *Oecologia* 74: 215–227.
- Thomson PC (1992) The behavioural ecology of dingoes in north-western Australia: III. Hunting and feeding behaviour, and diet. *Wildlife Research* 19: 531–541.
- Allen BL, West P (2013) The influence of dingoes on sheep distribution in Australia. *Australian Veterinary Journal* 91: 261–267.
- Fleming PJS, Allen BL, Allen LR, Ballard G, Bengsen AJ, et al. (2014) Management of wild canids in Australia: free-ranging dogs and red foxes. In: Glen AS, Dickman CR, editors. *Carnivores of Australia: past, present and future*. Collingwood: CSIRO Publishing. pp. 105–149.
- Allen BL, Allen LR, Engeman RM, Leung LK-P (2013) Intraguild relationships between sympatric predators exposed to lethal control: predator manipulation experiments. *Frontiers in Zoology* 10: 39.
- Allen BL, Allen LR, Engeman RM, Leung LK-P, (In press) Sympatric prey responses to lethal top-predator control: predator manipulation experiments. *Frontiers in Zoology*. xx: xx–xx.
- Johnson C (2006) *Australia's mammal extinctions: A 50 000 year history*. Melbourne: Cambridge University press.
- Purcell BV (2010) Dingo. *Australian Natural History Series*. Collingwood: CSIRO Publishing.
- Wallach AD, Ritchie EG, Read J, O'Neill AJ (2009) More than mere numbers: The impact of lethal control on the stability of a top-order predator. *PLoS ONE* 4: e6861.
- Kutsche F, Lay B (2003) *Field guide to the plants of outback South Australia*; Terry A, editor. Adelaide: Department of Water, Land and Biodiversity Conservation, Government of South Australia.
- Allen BL, Engeman RM, Leung LK-P (2014) The short-term effects of a routine poisoning campaign on the movement behaviour and detectability of a social top-predator. *Environmental Science and Pollution Research* 21: 2178–2190.
- Allen BL (2012) The effect of lethal control on the conservation values of *Canis lupus dingo*. In: Maia AP, Crussi HF, editors. *Wolves: Biology, conservation, and management*. New York: Nova Publishers. pp. 79–108.
- Yelland L (2001) *Holding the line: A history of the South Australian Dog Fence Board, 1947 to 2000*. Adelaide: Primary Industries and Resources South Australia.
- Allen BL (2012) Scat happens: spatiotemporal fluctuation in dingo scat collection rates. *Australian Journal of Zoology* 60: 137–140.
- West P (2008) *Assessing invasive animals in Australia 2008*. Canberra: National Land and Water Resources Audit, The Invasive Animals Cooperative Research Centre.
- Van Dyck S, Strahan R, editors (2008) *The mammals of Australia*. Third ed. Sydney: Reed New Holland.
- Allen BL, Read JL, Medlin G (2011) Additional records of small mammals in northern South Australia. *Australian Mammalogy* 33: 68–72.

42. Caughley G, Grigg GC, Caughley J, Hill GJE (1980) Does dingo predation control the densities of kangaroos and emus? *Australian Wildlife Research* 7: 1–12.
43. DEH (2009) 2010 Commercial kangaroo harvest quota report for South Australia. Adelaide: Department of Environment and Heritage, Government of South Australia.
44. Newsome AE, Catling PC, Cooke BD, Smyth R (2001) Two ecological universes separated by the dingo barrier fence in semi-arid Australia: Interactions between landscapes, herbivory and carnivory, with and without dingoes. *Rangeland Journal* 23: 71–98.
45. Cogger H (2014) Reptiles and amphibians of Australia (Seventh edition). Collingwood, Victoria: CSIRO Publishing.
46. Barrett G, Silcocks A, Cunningham R, Poulter R (2003) The new atlas of Australian birds. Hawthorn East, Victoria: Royal Australasian Ornithologists Union.
47. Triggs B (2004) Tracks, scats, and other traces: A field guide to Australian mammals (revised edition). Melbourne: Oxford University Press.
48. Brunner H, Triggs B, Ecobyte Pty Ltd (2002) Hair ID: an interactive tool for identifying Australian mammalian hair. Collingwood, VIC: CSIRO Publishing.
49. Klare U, Kamler JF, Macdonald DW (2011) A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Review* 41: 294–312.
50. Brillouin L (1956) Science and information theory. New York: Academic Press.
51. Pianka ER (1974) Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences, USA* 71: 2141–2145.
52. Newsome TM, Ballard G, Crowther MS, Fleming PJS, Dickman CR (2014) Dietary niche overlap of free-roaming dingoes and domestic dogs: the role of human-provided food. *Journal of Mammalogy* 95: 392–403.
53. Cupples JB, Crowther MS, Story G, Letnic M (2011) Dietary overlap and prey selectivity among sympatric carnivores: could dingoes suppress foxes through competition for prey? *Journal of Mammalogy* 92: 590–600.
54. Glen AS, Dickman CR (2008) Niche overlap between marsupial and eutherian carnivores: Does competition threaten the endangered spotted-tailed quoll? *Journal of Applied Ecology* 45: 700–707.
55. Glen AS, Pennay M, Dickman CR, Wintle BA, Firestone KB (2011) Diets of sympatric native and introduced carnivores in the Barrington Tops, eastern Australia. *Austral Ecology* 36: 290–296.
56. Mitchell BD, Banks PB (2005) Do wild dogs exclude foxes? Evidence for competition from dietary and spatial overlaps. *Austral Ecology* 30: 581–591.
57. Pascoc JH, Mulley RC, Spencer R, Chapple R (2012) Diet analysis of mammals, raptors and reptiles in a complex predator assemblage in the Blue Mountains, eastern Australia. *Australian Journal of Zoology* 59: 295–301.
58. Glen AS, Fay AR, Dickman CR (2006) Diets of sympatric red foxes *Vulpes vulpes* and wild dogs *Canis lupus* in the Northern Rivers Region, New South Wales. *Australian Mammalogy* 28: 101–104.
59. Letnic M, Dworjany SA (2011) Does a top predator reduce the predatory impact of an invasive mesopredator on an endangered rodent? *Ecography* 34: 827–835.
60. Allen BL (2011) Efficacy of para-aminopropiophenone (PAPP) to control dingoes (*Canis lupus* spp.) in the Strzelecki Desert of South Australia: Quinyambie field trial. Melbourne: Animal Control Technologies Australia.
61. Newsome TM, Ballard G, Fleming PJS, van de Ven R, Story GL, et al. (2014) Human-resource subsidies alter the dietary preferences of a mammalian top predator. *Oecologia* 175: 139–150.
62. Robertshaw JD, Harden RH (1986) The ecology of the dingo in north-eastern New South Wales, IV. Prey selection by dingoes, and its effect on three major prey species, the swamp wallaby *Wallabia bicolor*. *Australian Wildlife Research* 13: 141–163.
63. Marsack P, Campbell G (1990) Feeding behaviour and diet of dingoes in the Nullarbor region, Western Australia. *Australian Wildlife Research* 17: 349–357.
64. Di Marco M, Boitani L, Mallon D, Hoffmann M, Iacucci A, et al. (2014) A retrospective evaluation of the global decline of carnivores and ungulates. *Conservation Biology* 28: 1109–1118.
65. Wallach AD, Johnson CN, Ritchie EG, O'Neill AJ (2010) Predator control promotes invasive dominated ecological states. *Ecology Letters* 13: 1008–1018.
66. Carwardine J, O'Connor T, Legge S, Mackey B, Possingham HP, et al. (2011) Priority threat management to protect Kimberley wildlife. Brisbane: CSIRO Ecosystem Sciences.
67. Allen BL, Higginbottom K, Bracks JH, Davies N, Baxter GS, (In press) Balancing dingo conservation with human safety on Fraser Island: the numerical and demographic effects of humane destruction of dingoes. *Australasian Journal of Environmental Management* xx: xx–xx.
68. Hone J, Duncan RP, Forsyth DM (2010) Estimates of maximum annual population growth rates ( $r_m$ ) of mammals and their application in wildlife management. *Journal of Applied Ecology* 47: 507–514.
69. Newsome AE, Catling PC, Corbett LK (1983) The feeding ecology of the dingo. II. Dietary and numerical relationships with fluctuating prey populations in south-eastern Australia. *Australian Journal of Ecology* 8: 345–366.
70. Allen LR (2009) Best practice baiting: dispersal and seasonal movement of wild dogs (*Canis lupus familiaris*). Technical highlights: Invasive plant and animal research 2008–09. Brisbane: QLD Department of Employment, Economic Development and Innovation. pp. 61–62.
71. Allen LR (2010) Results of the wild dog movement and dispersal study. Beefy and the Beast Newsletter March 2010.
72. Newsome TM, Ballard G, Fleming PJS, Dickman CR (2011) When resources boom: learning from the story of dingoes in the Tanami Desert, Australia; Portland, USA.
73. Claridge AW, Mills DJ, Hunt R, Jenkins DJ, Bean J (2009) Satellite tracking of wild dogs in south-eastern mainland Australian forests: Implications for management of a problematic top-order carnivore. *Forest Ecology and Management* 258: 814–822.
74. Purcell BV (2009) Order in the pack: Ecology of *Canis lupus dingo* in the southern Greater Blue Mountains World Heritage Area [PhD]. Sydney: University of Western Sydney, School of Natural Sciences.