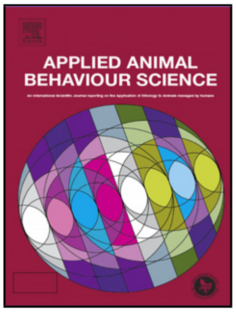

Title: Individual hunting behaviour and prey specialisation in the house cat *Felis catus*: Implications for conservation and management

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Highlights for Dickman-Newsome cat paper for Appl. Anim. Behav. Science:

1. Domestic house cats show individual preferences for different prey species

2. Hunting efficiencies of individual cats vary markedly among different prey species

3. Preferred prey species are hunted by cats irrespective of their density

4. Prey specialisation by cats may pose conservation problems for rare /threatened prey

5. Individual hunting behaviour may contribute to the predatory efficiency of cats

Individual hunting behaviour and prey specialisation in the house cat *Felis catus*: implications for conservation and management

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ABSTRACT

Predators are often classed as prey specialists if they eat a narrow range of prey types, or as generalists if they hunt multiple prey types. Yet, individual predators often exhibit sex, size, age or personality-related differences in their diets that may alter the impacts of predation on different prey groups. In this study, we ask whether the house cat *Felis catus* shows individuality and specialisation in its hunting behaviour and discuss the implications of such specialisation for prey conservation and management. We first examine the prey types killed by cats using information obtained from cat owners, and then present data on cat hunting efficiency on different prey types from direct observations. Finally, we quantify dietary shifts in cats when densities of their preferred prey vary. Our results suggest that cats can exhibit individual, or between-phenotype, variation in hunting behaviour, and continue to hunt specific prey types even when these prey become scarce. From a conservation perspective, these findings have important implications, particularly if cats preferentially select rare or threatened species at times when populations of these species are low. Determining whether prey specialisation exists within a given cat population should therefore be useful for assessing the likely risk of localised prey extinctions. If risks are high, conservation managers may need to use targeted measures to control the impacts of specialist individual cats by using specific baits or lures to attract them. We conclude that individuality in hunting behaviour and prey preference may contribute to the predatory efficiency of the house cat, and suggest that studies of the ontogeny and maintenance of specialist behaviours be priorities for future research.

Keywords: diet, feral cat, predator, predation, prey selectivity, prey switching

1. Introduction

Predatory animals are commonly placed into one of two categories depending on the variety of prey that they include in their diet. Specialist predators, on the one hand, consume a narrow range of prey and may be critically dependent on just one or two prey species (Erlinge et al., 1984). Such predators often have morphological or physiological adaptations that increase their hunting efficiency and ability to handle or process particular prey, but decrease their efficiency in tackling alternative prey. Examples include ant-mimicking spiders that so resemble their formicid prey in appearance, odour and behaviour that they can raid ant colonies with little risk (Castanho and Oliveira, 2009), frog-eating bats that use the specific calls of anurans to target their prey (Ryan, 2011), and myrmecophagous animals that use specialised structures (e.g. spade-like digging claws, long, sticky tongues) to expose and then consume subterranean termites or ants (Redford, 1987). On the other hand, generalist predators have relatively broad diets (Erlinge et al., 1984). Some generalists eat different prey types in rough proportion to their availability in the environment, consuming them either via bulk ingestion (e.g. baleen whales that consume krill, fish and other small marine organisms; Watkins and Schevill, 1979) or with the use of traps that indiscriminately catch diverse prey (e.g. orb-weaving spiders; Nentwig, 1985). Other generalists have broad diets, but prefer or select some types of prey more than others (Corbett and Newsome, 1987).

The specialist – generalist dichotomy is usually applied to populations or species of predators to describe how the animals behave collectively. In the case of specialists, all individuals in a population will show similar foraging behaviour and share a common, restricted diet. In the case of generalists, however, the broad dietary breadth exhibited by a population may arise in two ways.

Firstly, all members of the same population may have broad, generalised diets that include all components of the prey spectrum and thus differ little from individual to individual. Secondly, population members may each specialise on different components of the available prey spectrum. Here, individual animals behave as foraging specialists but the population, when viewed collectively, has a generalist diet. These two aspects of diet niche breath were distinguished by Van Valen (1965) and Roughgarden (1972, 1974a) and labelled, respectively, within-phenotype and between-phenotype components. Early research tended to emphasise the theoretical importance of these diet niche components, but empirical studies showed further that they could be employed to interpret patterns of foraging behaviour, competition and species composition in real world communities of fish, lizards, birds and other predators (Orians, 1971; Roughgarden, 1974a,b). Subsequent work has shown that predators often exhibit sex, size, age or personality-related differences in their diets (Brickner et al., 2014; Dickman, 1988), and that these differences can spread the impacts of predation across diverse communities of prey species (Bolnick et al., 2003; Yip et al., 2014).

Recent studies have uncovered between-phenotype foraging specialisations in populations of sea otters (Estes et al., 2003), guillemots (Woo et al., 2008), and sharks (Matich et al., 2011) and, increasingly, in large felids. For example, Ross et al. (1997) and Knopff and Boyce (2007) provided evidence of differential specialisation on deer *Odocoileus* spp. and bighorn sheep *Ovis canadensis* by individual cougars *Puma concolor* in Canada; Elbroch and Wittmer (2013) documented further individual-level hunting specialisations by the same species in Patagonia. Similar individual-level specialisation on different prey species has been shown within populations of jaguar *Panthera onca* (Cavalcanti and Gese, 2010), Amur tiger *Panthera tigris altaica* (Miller et al., 2013) and perhaps Eurasian lynx *Lynx lynx* (Odden et al., 2006). Individuality in predator hunting behaviour may arise as a learning process when young animals are being taught about sources of food by parents (Kuo, 1930; Woo et al., 2008), when independent animals discover new sources of prey or hunting locations (Cook et al., 2006), or if declines in prey numbers force animals to exploit different components in the remaining prey base (Svanbäck and Bolnick, 2005, 2007). Individual-level dietary specialisation by predators on particular prey can have dramatic effects on food web dynamics (Tinker et al., 2008) and, if preferred prey species are already scarce or threatened, targeted predation may place them at heightened risk of local extinction (Petorelli et al., 2011). Felid predators pose particular problems for livestock if they learn to specialise on them (e.g. Linnell et al., 1999); in settled areas, rogue felids sometimes hunt and kill companion animals and may even target people themselves (Frump, 2006).

In this study, we ask whether the house cat *Felis catus* shows similar individuality in its hunting behaviour to some of its larger relatives, and marshal evidence from several disparate studies to address this question. We focus on the house cat for several reasons. Firstly, *F. catus* is ubiquitous. It is kept as a house pet or used as a pest control agent on every continent except Antarctica, and has established un-owned, stray or feral, populations worldwide (Denny and Dickman, 2010). Secondly, both domestic and un-owned cats have been shown to exact an enormous toll on wildlife. In the United States (US), for example, Dauphiné and Cooper (2009) concluded that cats kill over a billion birds annually. Loss et al. (2013) estimated further that cats kill 1.4 – 3.7 billion birds and 6.9 – 20.7 billion mammals each year in the US, with 69% of bird deaths and 89% of mammal deaths caused by un-owned cats and the remainder by their domestic counterparts. In Canada, Blancher (2013) put the annual loss of birds to cats at 100 – 350 million, with most falling victim to feral cats. Thirdly, there is some evidence that cats may develop marked individuality in hunting and killing behaviour, targeting such unusual prey as small bats (Ancillotto et al., 2013) and potentially putting rare species at particular risk. For example, no more than four cats were implicated by Gibson et al. (1994) in the demise of the rufous hare-wallaby *Lagorchestes hirsutus* at reintroduction sites in the Tanami Desert of central Australia, and a similar number of cats is thought to have extirpated the endemic wren *Traversia lyalli* on Stephens Island, New Zealand, within five years of their introduction (Atkinson and Bell, 1973; Galbreath and Brown, 2004). The predatory impacts of cats are notoriously difficult to manage (Denny and Dickman, 2010;

Dickman, 2014; Loyd and DeVore, 2010). By understanding how cats hunt, and the extent to which they show individuality in hunting behaviour, we can gain clearer insight into both management tactics and strategy.

Based on the studies cited above, it is reasonable to expect that populations of house cats may show between-phenotype variation in hunting behaviour and preferences for particular prey types, and will do so irrespective of prey abundance. Given these expectations, we derive and test three contingent hypotheses. Thus, within cat populations we predict that:

1) Individual cats will show distinct preferences for particular prey types,
2) Individual cats will vary in the efficiency with which they hunt different prey types, and
3) Preferred prey will be targeted by cats irrespective of prey density.

We use our results to provide suggestions for managers who are charged with controlling cat-impacts.

2. Materials and methods

To test the three hypotheses, we present observations of both domestic and un-owned cats using different techniques in a wide variety of locations. The methods used to test each hypothesis are described separately below. We confirm that all procedures comply with the ethical guidelines of the International Society for Applied Ethology (Sherwin et al., 2003).

2.1. Hypothesis 1: Do individual cats show distinct preferences for particular prey types?

To assess whether cats show preferences for particular types of prey, we studied a sample of domestic cats in suburban Sydney, Australia, using information obtained from the cats' owners. Following the pioneering studies of Paton (1990, 1991), potential participants were contacted initially by letter-drops to residential post boxes, and people in residences with one or more cats were invited to take part in a further questionnaire survey. The areas targeted for the survey were in the city's eastern suburbs within a 0.5 km radius of four adjacent bushland reserves ranging in size from 1.2 – 18 ha (Fig. 1). These reserves – Cooper Park, Harbour View Park, Trumper Park and the Thomas Hogan Reserve – were selected because preliminary observations indicated that they contained diverse populations of potential prey for cats (e.g. reptiles, birds, introduced rodents, native marsupials), and also that cats frequently hunted there (Dickman, 2009). Residents who agreed to participate were asked a series of questions about the age, sex, breed, reproductive status (sterilised or intact) and number of cats in their care, whether the cats had regular and reliable access to food, whether the cats were free to roam by day or night, and whether cats returned captured prey animals to the owners' homes. Residents were also asked if they would be prepared to collect or record the prey animals that their pets killed and returned over the course of a year. Surveys were carried out in 1993-94 and 1997-98 and we pooled the results of both surveys for analysis. We present a subset of the overall results here, and summarise only the data on prey that were returned by cats that had no restrictions placed on their movements or temporal activity by their owners.

To determine whether predators prefer particular prey, the types of prey killed should ideally be compared with the availability of those types in the environment (Knopff and Boyce, 2007). However, when prey types vary markedly in their activity, habitat use and behaviour, as may be expected of prey in the different classes of vertebrates, their relative availability to predators is difficult to measure and comparisons between groups become unreliable (Spencer et al., 2014). In this study, we made no attempt to document the availability of the different prey groups. However, as our study cats had access to essentially the same suite of prey in the four co-located reserves, we assumed that any differences detected in the prey they killed arose due to differences in preference rather than availability. A further assumption we made was that cats would return a representative sample of prey to their owners. Domestic cats can be expected to consume some prey and to leave other prey *in situ* after subduing it, and hence may return only a fraction of the prey that they kill (e.g. Baker et al., 2005; Lepczyk et al., 2003; Tschanz et al., 2011). However, we were less interested in the numbers of prey than in the types of prey that cats kill, and note that the distribution of prey types returned to owners was similar to that in the diet of cats in the survey area (Dickman, 2009).

2.2. Hypothesis 2: Do individual cats vary in the efficiency with which they hunt different prey types?

We tested this hypothesis by making direct observations of hunting cats at five different locations in England and Australia. The first location, at Shotover Country Park, near Oxford, UK, comprises a mosaic of wooded and cleared areas on rolling hills that provide high vantage points. This site contains a diverse array of mammals and birds as well as several species of reptiles (Dickman, 1987; Whitehead et al., 2010), and was visited either once or twice a week for 5 – 6 h on each occasion between April and July, 1983. In Australia, observations of cats were made in the Simpson Desert, Queensland, at North Head, New South Wales, and near Kellerberrin and on Rottnest Island, Western Australia (Fig. 1) for intensive periods of 5 – 8 days at different times between March 1986 and May 2008, with observations lasting 3 – 5 h on each occasion. Observations in the Simpson Desert were made near Ethabuka homestead in open sand dune habitat dominated by spinifex *Triodia basedowii* grassland (Dickman et al., 2014). The North Head site comprises dense coastal heath, forest and open cleared areas (Scott et al., 1999), as does the site on Rottnest Island, although most observations at the latter site were made in open reforestation plots near the Rottnest Island Biological Research Station (Dickman, 1992). At Kellerberrin, observations of cats were made in remnant woodland in Ryans Reserve (Smith et al., 1997). All the Australian sites contain small or medium-sized (<5 kg) native mammals, introduced mammals such as rabbits *Oryctolagus cuniculus*, black rats *Rattus rattus* or house mice *Mus musculus*, and diverse assemblages of birds and reptiles.

In all the study locations, cats were probably un-owned. We confirmed in discussions with the managers of the only properties within a radius of ~9 km of Ryans Reserve and > 50 km of Ethabuka homestead that they did not own pet cats, and cat-ownership was prohibited at the other sites owing to their status as sites protected for conservation. In consequence of this, cats at each location likely obtained most or all of their food from hunting. However, because of their proximity to human settlement, the cats in each location were accustomed to human presence and could be observed at distances of ≥10 m without any evident effect on their behaviour or activity. By selecting elevated vantage points on the sides of hills above where cats were detected, it was then possible to observe hunting behaviour and score both successful and unsuccessful kill-attempts. These locations also allowed us to shift, as needed, from point to point on the hillsides to keep individual cats in view as they moved. We used binoculars to aid observations so that hunting attempts by cats could be detected and scored even in habitats with heavy ground cover. At four locations we made most observations (> 95%) by day or at or just after dusk as initial searches at night failed to find any cats that were active. At North Head, however, pilot searches indicated that some cats were active in the first half of the night, and here nearly half of all observations (14/29) were made after dusk but before midnight under dim white light or red light. Photographs were taken of all cats that were observed, and this allowed us to tally the number of strikes they made on potential prey on an individual basis. We express the hunting efficiency of individual cats for different prey types simply as the percentage of capture attempts that resulted in a successful kill.

2.3. Hypothesis 3: Are preferred prey targeted by cats irrespective of prey density?

Two of the above study locations, Ryans Reserve and Ethabuka, were used to test our third hypothesis. Initial observations of cats in these locations and analyses of their diet from collected scats (see below) indicated that rabbits were preferred prey for most individuals, and smaller mammals, birds and lizards collectively formed a minor part of the diet (< 20% by scat volume at Ryans Reserve; ~ 35% by volume at Ethabuka). At Ryans Reserve, rabbits occurred in the reserve itself but were present in much greater numbers in land surrounding the reserve that was used for wheat cropping and sheep grazing. To keep their numbers at levels where crop damage was tolerable, local landholders baited rabbits irregularly with oats laced with the toxin sodium fluoroacetate, or 1080. Baits were set twice during our two and half year study at Ryans Reserve, reducing rabbit numbers dramatically on each occasion. At Ethabuka, rabbits were localised near the homestead and two further specific sites around natural water springs to the north and south of the homestead. No baits or other control measures were established at these locations, but rabbit numbers in this arid environment fluctuated depending on the amount of rain that fell during the summer rainy season. During our four year study at this location, from mid-1990 to mid-1994, summer rainfall (November – February) varied from 98 mm in 1992-93 to 439 mm in 1990-91 (Dickman et al., 2010), with rabbit numbers generally rising within 4 – 6 months of heavy rainfall events and falling again within a year as conditions dried out.

We used spotlight counts along standardised transects to obtain an index of rabbit numbers at each location, using either a single 100 W spotlight (Ryans Reserve) or two spotlights (Ethabuka) from a vehicle moving at 10-15 km/h. Transects were traversed after dusk when rabbits were active, at random times between 20:30 h and 01:00 h, and were restricted to calm, dry conditions when good visibility was assured. Although spotlight counts can be biased if carried out between different habitats and under different environmental conditions (Newsome et al., 2014; Vine et al., 2009), we assume that detectability of rabbits was relatively constant here owing to the open nature of the habitat in each study location and our attempts to ensure comparability in the conditions under which observations were made. The transect at Ryans Reserve was ~10 km long and that at Ethabuka ~12 km; two replicate counts were made along each transect on 3-6 visits to each location for each year of the respective studies. Counts were averaged each sampling session and standardised to yield an estimate of rabbits seen per km.

Cat scats were collected on each sampling occasion along the spotlighting transects, from walking tracks at each location and from rabbit warrens; the same sites were searched on each occasion to increase confidence that scats had been produced in the interval since the previous sampling occasion. Scats from the first sampling session at each location were discarded as their age was unknown. Collected scats were placed in individually labelled bags, dried and later pulled apart in the laboratory to identify prey that been consumed. Mammals were identified from teeth, claws or hair, birds from feathers, beaks or claws, reptiles from scales and often from hard remains such as feet, and invertebrates from mouthparts, antennae, legs and other hard parts of the exoskeleton; plant remains were noted but not identified further. Only mammals were identified to species, with identification relying principally on the external characteristics and cross-sectional appearance of hair (Brunner and Triggs, 2002). We estimated the volumetric contribution of different prey types in each scat by eye, but for simplicity present dietary results as the percentage frequency of occurrence (the number of samples containing a specific prey type divided by the total number of samples × 100).

2.4. Data management and statistical analyses

Preliminary inspection of the questionnaire survey results (hypothesis 1) showed that only some cats returned prey to their owners, and also that many cats returned too few prey to determine any dietary pattern. Hence, analyses were restricted to those cats that presented ≥ 10 individual prey items to their owners over the duration of the study. To identify similarities and differences in the prey that cats that returned, we first grouped prey into nine categories: rat, common ringtail possum *Pseudocheirus peregrinus*, common brushtail possum *Trichosurus vulpecula*, large bird, small bird, lizard, reptile (other), frog, and invertebrate. From the records provided by respondents it was not possible to reliably split the non-mammalian groups into finer categories. However, the large bird category comprised largely corvids and the crested pigeon *Ocyphaps lophotes*, all of which were distinguished by respondents. For analysis, we constructed a matrix of Bray-Curtis dissimilarities of the prey captured by cats, after first standardising the prey data to 1.0 for each cat by dividing the number of each type of prey returned by the total number. Standardising reduced any confounding effects of differing sample size between cats (Quinn and Keough, 2002). The matrix was then subjected to ordination by non-metric multidimensional scaling (nMDS). We used two dimensions to improve interpretability of the ordination, and used the lowest stress value from 20 random starts (Quinn and Keough, 2002). To further assess the association between individual cats and the prey that they captured, a chi-squared contingency test was computed using the raw frequency data. Finally, for descriptive purposes we calculated a simple measure of the diversity of prey types returned by cats based on Simpson's diversity index, D:

$$D = \sum \left\{\frac{ni(ni-1)}{N(N-1)}\right\}$$

where n_i = the number of individuals in the ith prey type, and N = the total number of individuals. Expressed as the complement (1 – D), Simpson's index is 0 if only one prey type is present and approaches 1 if there are many. While simple, this index is intuitive and robust (Magurran, 2004).

The hunting efficiencies of individual cats (hypothesis 2) were quantified by comparing the numbers of prey in each category that were observed to be successfully versus unsuccessfully attacked and, for cats with ≥ 10 observations, differences between prey types detected using chi-squared contingency analyses. Tests of hypothesis 3 were made by plotting the percentage frequency of occurrence of rabbit in cat scats against estimates of rabbit abundance at different sampling times in the two study locations; curves of best fit were evaluated simply by improvement in R^2 (Quinn and Keough, 2002). Non-metric multidimensional scaling was implemented in PRIMER v. 5 (Clarke and Warwick, 1994) and other analyses in SPSS v. 15.0 (SPSS, 2006).

3. Results

3.1. Hypothesis 1: Do individual cats show distinct preferences for particular prey types?

Overall, 362 people responded from a total of 779 letter-drops, giving a response rate of 46%. Of the respondents, 159 people (44%) owned cats that had potential access to the bushland reserves and agreed to keep a log of the prey that their pet returned; of these, 105 people actually did so. At least 51 cats were reported as returning no prey to their owners, with the dataset presented below comprising 62 cats (six people returned information on 2 – 3 cats under their care).

These animals comprised 34 females and 28 males, all neutered, and aged from 1-12 years at the beginning of the study. Records of the prey returned by these cats were collected over periods of 7-13 months.

In total, the cats returned 667 prey items to their owners, with a range of 1-58 per individual. Small birds were returned most often, by 41 cats ($n = 245$, $\bar{x} = 3.95 \pm 6.65$ SD, range 0-29 per cat). The superb fairy-wren *Malurus cyaneus*, eastern yellow robin *Eopsaltria australis*, welcome swallow *Hirundo neoxena*, and rainbow lorikeet *Trichoglossus haematodus* were among the most commonly reported native birds, as was the Indian myna *Acridotheres tristis* among the introduced species. Lizards were returned by 33 cats ($n = 162$, $\bar{x} = 2.61 \pm 5.57$ SD, range 0-28 per cat) and comprised the skinks *Lampropholis delicata*, *L. guichenoti*, *Saproscincus mustelinus* and *Eulamprus quoyii*. Rats were returned by 28 cats ($n = 131$, $\bar{x} = 2.11 \pm 5.24$ SD, range 0-34 per cat); all were probably black rats *Rattus rattus*, as no other *Rattus* species are known to occur in the survey area. Large birds were returned by 10 cats ($n = 40$, $\bar{x} = 0.65 \pm 2.14$ SD, range 0-11 per cat) and invertebrates (including blattids, phasmids and large scolopendrid centipedes) by 23 cats ($n = 55$, $\bar{x} = 0.89 \pm 1.56$ SD, range 0-7 per cat). Frogs and the two species of possum were returned infrequently, by 5-8 cats in each case; one cat returned three ringtail possums and another cat returned six frogs (probably *Limnodynastes peronii*). Three reptiles in the 'other' category were returned. All were snakes; one was a golden crowned snake *Cacophis squamulosus*, another a juvenile green tree snake *Dendrelaphis punctulatus*, and the third was not identified.

Twenty-six cats returned 10 or more prey items to their owners, with very marked differences in the prey types that were represented ($\chi^2_{100} = 987.95$, $P < 0.001$; data on the two species of possum, 'other' reptiles and frogs were omitted from analysis due to insufficient numbers). Ordination identified five groups within this subset of cats, four that exhibited some degree of specialisation on particular types of prey and one where no clear specialisation could be identified (Fig. 2). The largest group ($n = 8$) comprised cats that captured small birds. Small birds comprised 66.7-100% of the prey returned by these cats, and resulted in a prey-take diversity (1-*D*) of 0.23 ± 0.18 SD. Five cats focused on lizards (87.5-94.4% of the prey items returned, 1-*D* = 0.16 ± 0.05 SD), four on rats (81.8-97.1% of prey items returned, 1-*D* = 0.18 ± 0.11 SD) and three on large birds (70-90% of prey items returned, 1-*D* = 0.30 ± 0.14). Six cats showed no evident specialisation on any prey type, returning 4 – 6 types of prey to their owners and with no prey type representing more than 55% of their catch. The diversity value for these cats (1-*D* = 0.68 ± 0.04 SD) was greater than that for all other groups identified in Fig. 2 (one-factor ANOVA, $F_{4,21} = 17.22$, $P < 0.001$), but there was no difference among the four groups that predominantly captured and returned one type of prey (Tukey *post hoc* tests, $P = 0.43\text{-}0.99$ for all between-pair comparisons).

3.2. Hypothesis 2: Do individual cats vary in the efficiency with which they hunt different prey types?

In total, we recorded 182 hunting attempts by 15 cats across the five study locations in > 400 h of field observation (Table 1). Most observations were made while waiting for animals to appear, but about 20% of observations were made opportunistically. Nine cats were observed to make ≥ 10 attacks on prey and, of these, four exhibited greatest efficiency (83-100% of attacks successful) when hunting rodents, and one was most efficient (94%) when hunting rabbits (Table 1). These individuals achieved maximal success of 50% when hunting any other types of prey. The remaining cats hunted two or three types of prey with similar efficiency (Table 1).

It was not always clear if a prey item was killed in a successful attack; rodents, in particular, were often subdued and ‘swatted’ repeatedly by a cat’s forepaws while still alive. Prey items were usually carried away or eaten, but on 12 occasions they were left *in situ* after they had stopped moving. Two cats (numbers 2 and 3, Table 1) used cleared patches in long grass to stalk field voles *Microtus agrestis* and occasionally bank voles *Myodes glareolus*, cat 6 adopted a sit-and-wait strategy to pounce on house mice from behind dense grass or shrub cover, while cat 15 waited at entrances to the burrows of long-haired rats *Rattus villosissimus* and actively hunted rats after they emerged. The rabbit specialist cat, number 4 (Table 1), adopted a similar strategy of sitting near entrances to warrens and pursuing rabbits that emerged.

3.3 Hypothesis 3: Are preferred prey targeted by cats irrespective of prey density?

We collected 329 cat scats at Ryans Reserve (5 – 63 on each sampling occasion) and 271 at Ethabuka (5 – 35 on each sampling occasion). Analyses of these scats showed that cats at both study locations ate a broad range of prey, with native small mammals, birds, lizards and invertebrates comprising, variously, 5-83% by frequency of occurrence on any given sampling occasion. However, rabbits dominated the diet; they were represented in > 50% of cat scats on most sampling occasions, falling exceptionally to 33% by frequency of occurrence in scats at Ryans Reserve and to 8% by frequency of occurrence at Ethabuka. Plots of rabbit in the diet of cats against rabbit abundance suggested that cats continued to consume rabbits even when rabbit numbers were low, with this effect being more evident at Ryans Reserve than at Ethabuka (Fig. 3). The curves of best fit in each study location were second-order polynomial (quadratic) relationships, accounting for 57% of the variance in the data at Ryans Reserve and for 42% at Ethabuka (Fig. 3). These models indicate that rabbits occurred in 49% of cat scats at Ryans Reserve and 25% of cat scats at Ethabuka when rabbit numbers were so low that they were not detected in spotlight surveys (Fig. 3a, b). At Ryans Reserve the frequency of rabbit in the diet dropped sharply when fewer than 3.5 rabbits were observed per km of transect (Fig. 3a), but a similar threshold was not evident at Ethabuka (Fig. 3b). The numbers of rabbits counted and numbers of cat scats collected were correlated at both sites (Ryans Reserve, $r = 0.78$, df = 12, $P < 0.001$; Ethabuka, $r = 0.74$, df = 11, $P = 0.004$), indicating a positive relationship between cat activity and their preferred prey.

4. Discussion

The results reveal some between-phenotype variation in hunting behaviour and preferences for particular prey types by cats, and thus provide some ostensible support for each of our three hypotheses. These findings contribute to a growing body of evidence showing individuality in foraging behaviour across a wide range of disparate taxa (Araújo et al., 2011; Masello et al., 2013; Ropert-Coudert et al., 2003), and extend suggestions that have been made previously about hunting specialisations in the house cat (Bradshaw, 2013; Dickman, 2009; Mendl and Harcourt, 1988).

Domestic cats usually have their resource requirements met by their owners, and there was no indication that any of the cats in the questionnaire surveys were deprived of either food or shelter. Yet, many cats captured and returned prey items to their owners. The 62 cats that provided data were drawn from a larger sample of 113, suggesting that only 55% of the study population actually hunted wild prey. However, owners of at least 22 of the 51 cats that ostensibly returned no prey failed to provide any documentary evidence of nil-take despite suspecting that their cats may hunt, and it is possible that the percentage of hunters in the sample was greater than 55%. For example, Paton (1991), Kays and DeWan (2004) and Loss et al. (2013) reported that 50% – 80% of cats in their surveys hunted live prey, and noted further that only a third to a half of all prey that was captured or killed was likely to be returned to their owners. Small mammals dominated the catch in these latter studies, whereas small birds were the dominant prey type here. These differences most likely reflect the relative lack of small mammals in the reserves that we studied, where the introduced black rat is the only small mammal that occurs (Banks et al., 2011).

Despite being reported by their owners to be well fed and to have access to wet or dry food *ad libitum*, at least some domestic cats clearly hunt live prey and appear to show distinct differences in the types of prey that they hunt. Our sample of cats was relatively small – 26 individuals – but could be split into four groups that each returned predominantly one type of prey and a fifth group that returned a greater diversity of prey types. Several explanations can be advanced to account for these observations.

In the first instance, prey return data are subject to several potential biases including mis-identification of prey, under-reporting by survey participants (van Heezik et al., 2010), underestimation of the numbers of prey that are killed (Kays and DeWan, 2004; Loyd et al., 2013; Woods et al., 2003), and differences in palatability among prey types that may determine whether they are eaten or returned to their owners (Blancher, 2013; Krauze-Gryz et al., 2012). However, while these potential sources of bias probably affected the numbers of prey items returned in our study, it is less likely that they contributed greatly to the marked between-cat differences in prey types that we found to be returned. Thus, small birds, rats, lizards and invertebrates were the prey types most frequently returned and eaten by cats in the survey area (Dickman, 2009); frogs were the only category of prey that were returned to cats' owners but not found in the diet (Dickman, 2009). Using animal-borne video cameras, Loyd et al. (2013) showed further that neither habitat nor prey size were related to whether cats left prey where they had been killed or brought them home. Based on these considerations, we suggest but cannot confirm that our findings of individual-level differences in prey types returned by cats to their owners have not been greatly biased by the problems inherent in prey-return surveys, and follow Loyd et al. (2013) in advocating the use of animal-borne cameras as a means of obtaining more reliable information.

Secondly, it is possible that, despite our supposition that all cats had roughly equal access to the different prey groups, individuals actually used small areas of the bushland reserves and hunted particular prey that were localised there. Although the reserves are small (≤ 18 ha), domestic cats do not always exhibit extensive movements and may be restricted to areas of < 1 ha (Barratt, 1997a; Kays and DeWan, 2004). However, several studies of domestic cat movements in suburban areas near bushland show that some cats move over areas of several hectares each day and recommend excluding cats from buffer zones 0.3 – 1.2 km wide around bushland reserves if these remnants are to be protected from cat-impacts (Lilith et al., 2008; Metsers et al., 2010; Thomas et al., 2014). In the present study, with the exception of the ringtail possum which was known to occur in just one section of Cooper Park, all the prey types hunted by cats appear to be widely distributed in the reserves and also were often present in the gardens of the cats' owners.

A further possible explanation for the consistent differences in prey that individual cats returned (Fig. 2) is that they arose from differences in cat sex, age or breed as have been reported in domestic dogs (Mehrkam and Wynne, 2014). However, this also seems unlikely: cats have been much less subject to artificial selection for size, shape or behaviour than their canine counterparts (Bradshaw, 2013), and cats of different sex, age or breed often comprised the different groups that we were able to distinguish. Loyd et al. (2013) also found no evidence that cat age, sex or habitat influenced hunting behaviour.

Taken together, we suggest it is most plausible that cats within the different groups (Fig. 2) preferred particular prey, and selected them while hunting to the relative exclusion of other potential prey types. In a comparable study in suburban Canberra, Barratt (1997b) reported cats to take just 2.8 prey species per individual from a prey base of at least 67 different species; Barratt (1997b) did not mention individual-level specialisation, but his results support this interpretation. By contrast, Loyd et al. (2013) found little evidence of individual-level specialisation on prey by cats in north-eastern Georgia, although no cat in that study was seen to capture more than five prey.

Our observations of hunting attempts by cats support the idea that individuals exhibit different prey preferences, and may achieve greatest hunting efficiency by focussing on particular prey types. None of the cats we observed hunting were far from human settlement (~1 – 6 km), but they were almost certainly not owned by local people and would have obtained most or all of their food by active hunting. They were, however, familiar enough with people to allow approaches to within 10 m before taking flight. Although many observations were made at about this distance, some observations were made at greater distances with the observer under cover and apparently undetected by the quarry, with no evident differences in the hunting behaviour of individual cats being observed. We are therefore confident that the hunting behaviours we report have not been biased overtly by observer presence. As we also attempted to observe our study cats at times when they were active, we have some confidence that we did not miss many hunting forays that occurred when we were not present, and hence suggest that our observations of hunting behaviour were not greatly biased by the timing of our observations.

Of the 15 cats we observed hunting, five exhibited greatest efficiency in hunting rodents or rabbits, and used different hunting tactics to capture these prey. These tactics were often used to hunt other prey types, albeit unsuccessfully. For example, the two cats that successfully used stalking (Turner and Meister, 1988) to hunt voles were observed to flush small birds when stalking them and also conveyed their presence to rabbits in time to allow the rabbits to bolt to their burrows. The rabbit specialist, conversely, used a sit-and-wait strategy (Turner and Meister, 1988) to attack rabbits soon after they emerged from burrows. It appeared slow to respond to lizards that it detected on or near the rabbit warrens that it staked out, and moved its body or tail in the presence of birds and thus forewarned these potential prey of an impending attack. In contrast, other cats that successfully captured different prey types usually adopted varied hunting tactics to do so. Our sample sizes for some cats were too small to reliably describe their hunting behaviour, but the results for frequently observed individuals suggest that both specialists and generalists were probably present in the study cat populations.

Observations of cat diet at two study locations, Ryans Reserve and Ethabuka, indicated that cats continued to hunt their preferred prey – rabbits – when rabbit numbers varied widely. However, when numbers of rabbits fell to low levels, consumption of rabbits declined. At Ryans Reserve cats ate fewer rabbits when the observed numbers fell below 3.5 per kilometre of transect, but rabbit remains were still found in at least a third of cat scats even when no rabbits were evident during our surveys. This pattern, suggestive of a type-2 functional response by cats to changing densities of their preferred prey (Molsher et al., 1999), is indicative of a specialist dietary predator, albeit one that will consume alternative prey when its preferred prey becomes progressively unavailable. A similar pattern was observed at Ethabuka, although rabbits were consumed less frequently there when this prey type became scarce. Rabbit abundance did not achieve the high levels at this site that were recorded at Ryans Reserve (Fig. 3), and it is possible that fewer cats specialised on rabbits at this location. Unfortunately, we do not have information on the abundance of other prey species during the periods of low rabbit numbers and cannot say whether cats switched to alternative food sources because other prey were more abundant at these times or became scarce themselves. At Ethabuka, plots that were monitored for small vertebrates ~25 km away from the sites used in the present study showed that most small vertebrates declined within a year of rain-induced increases in primary productivity, and that cats declined several months after this (Dickman et al., 2014). This may suggest that cats exploit their preferred prey until it reaches very low levels before switching to alternative prey, but does not allow us to say whether specialists or generalists in the cat population are more likely to persist. Catling (1988) and Yip et al. (in press) showed that some cats can switch to hunting alternative prey if their preferred species are not available, while Elmhagen et al. (2000) noted that specialist predators generally show pronounced numerical declines when their preferred prey become scarce. In our study, we found fewer cat scats when rabbits declined, suggesting that cat populations probably declined when rabbits became scarce. We speculate that specialists would have fared most poorly from the decline in rabbit populations, but caution that more data are required to confirm this. Hence, support for our third hypothesis remains equivocal.

From a conservation and management point of view, our results indicate the utility of determining the relative numbers of specialist and generalist predators in a given cat population. For example, if prey specialisation dominates there may be considerable risk of localised extinctions of preferred prey. In addition, if any prey species are of conservation concern, general attempts to control cat numbers may do little to alleviate the risk of localised extinction if the individual cats that specialise on these prey species are not controlled. Targeted control of individual cats elevates the challenge of managing cat-impacts, which is already difficult. However, shooting has been used to effectively remove small numbers of individual cats (Bester et al., 2000; Read and Bowen, 2001), and different lures and baits show some promise in attracting individual cats which may then be trapped.

For example, Mahon (1999) used toy mice to attract cats that were depredating populations of small rodents, and succeeded in removing sufficient rodent-hunting cats to allow increases in one of his target species. Lures based on auditory, visual or olfactory attractants have been shown to be effective in certain situations (Hanke and Dickman, 2013; Molsher, 2001; Moseby et al., 2004), with cats being variably and individually responsive to particular attractants. Baits comprising remains of target prey species (e.g. rabbits) have also been used to successfully trap cats. For example, Molsher (2001) captured most cats in traps with fresh rabbit carcass as bait, and noted that cats were likely to be attracted to this bait as rabbits were the main – and thus most familiar prey – in her study.

When considering the impacts of house cats, even a population of generalists could threaten prey species if the overall predation pressure across a range of species is intense. Our finding that cats in two locations showed some preference for rabbits, even when rabbit numbers declined, also presents a dilemma in the Australian context because rabbits are a significant biodiversity pest (Newsome, 1990). Indeed, accelerated increases in rabbit abundance have been demonstrated where cats and red foxes *Vulpes vulpes* were experimentally removed in a field experiment in central New South Wales (Newsome et al., 1989). Therefore, in areas where cats specialise on rabbits, integrated pest management strategies that target both rabbits and cats are likely to be required (Newsome, 1990). If successful, the potential for negative effects associated with prey switching may then be reduced. However, cat control remains challenging, especially at large scale.

In the absence of a proven method to control cats over large areas (Denny and Dickman, 2010), prey selection by cats should be a focus of research for conservation managers. In particular, we note the very limited knowledge of whether prey specialists or generalists have a greater chance of survival during periods when particular prey species decline. There is also little understanding of the ontogeny of prey preference, the maintenance of preferences, or of prey switching behaviours by cats. We suggest that these should be priority areas for further research. Nonetheless, our study does suggest that prey specialisation by cats occurs and that populations of cats exhibit some between-phenotype variation in hunting behaviour. This is consistent with studies on larger felids showing similar levels of specialisation on different prey species (e.g. Cavalcanti and Gese, 2010; Miller et al., 2013; Odden et al., 2006), and indicates that variation in individual hunting behaviour and prey specialisation may be common phenomena among felid populations.

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Table headers and figure captions:

Table 1 Hunting success of individual house cats *Felis catus* taking four different categories of prey, shown as the % of successful attacks per prey category. Numbers in brackets represent the numbers of attacks observed on prey in each category.

Fig. 1 Map of eastern Sydney, Australia, showing the four bushland reserves (study sites) and surrounding areas used to test the hypothesis that individual cats will show distinct preferences for particular prey types. Inset: map of Australia showing other locations used in this study. (Note: North Head and Ryans Reserve are not shown, but are close to Sydney and Rottnest Island, respectively).

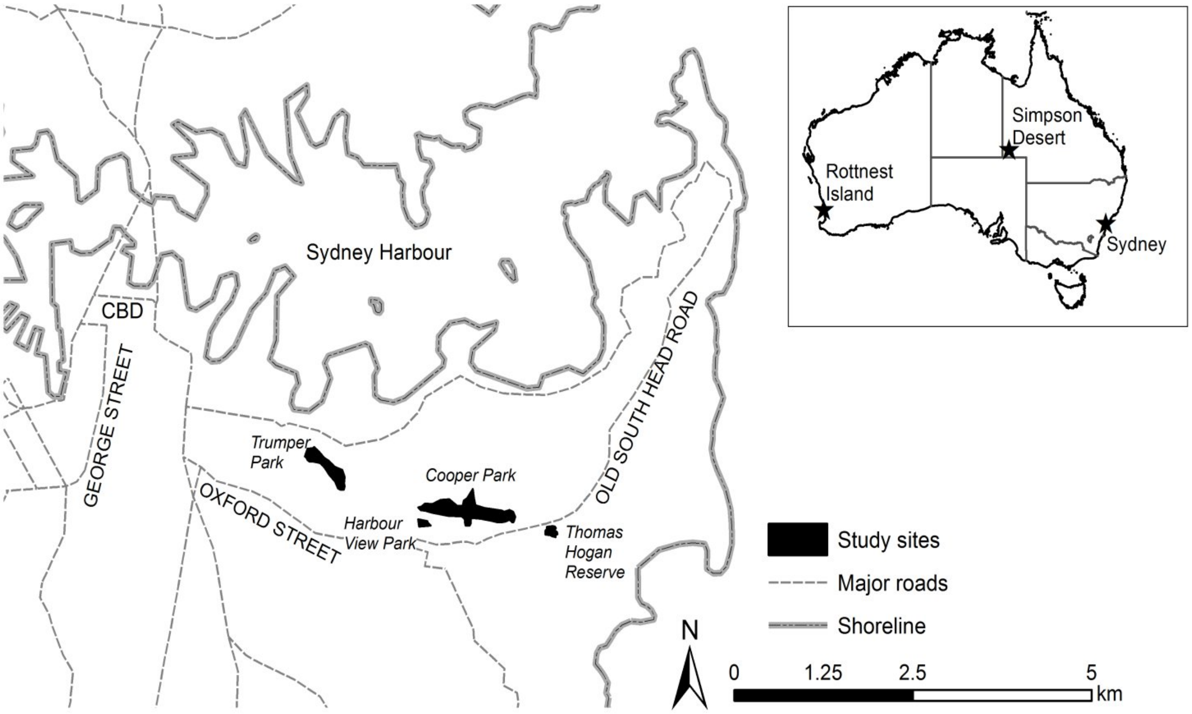
Fig. 2 Two dimensional ordination (stress = 0.14) of major types of prey returned by domestic house cats *Felis catus* to their owners living around bushland reserves in Sydney, Australia. Data are based on 26 cats that returned ≥ 10 prey items over the course of study.

Fig. 3 Frequency of occurrence (%) of rabbit in the diet of house cats *Felis catus* in relation to rabbit abundance (numbers observed by spotlight along transects, standardised per km) at two study locations. Top panel (a) Ryans Reserve, Western Australia, quadratic regression: $y = 48.70 + 5.73x - 0.17x^2$, $R^2 = 0.57$, $P = 0.010$; bottom panel (b) Ethabuka, Queensland, quadratic regression: $y = 24.92 + 16.53x - 1.20\ x^2$, $R^2 = 0.42$, $P = 0.066$.

Table 1 Hunting success of individual house cats *Felis catus* taking four different categories of prey, shown as the % of successful attacks per prey category. Numbers in brackets represent the numbers of attacks observed on prey in each category. The total number of observations made per cat, and the time taken to make the observations, are also shown.

			% of successful attacks on:				
Cat no.	Total no. of observations	Time (h)	Rodent	Rabbit	Bird	Lizard	χ^2
1	17	27	75 (8)	40 (5)	75 (4)		1.89
2	22	67	100 (14)	0 (4)	25 (4)		18.54***
3	15	44	83 (6)	0 (3)	17 (6)		8.06*
4	26	36		94 (16)	25 (4)	33 (6)	11.82**
5	8	16			50 (2)	83 (6)	-
6	11	7	100 (5)		0 (2)	50 (4)	6.68*
7	7	10	100 (4)		50 (2)	0 (1)	-
8	8	18	100 (4)		50 (2)	50 (2)	-
9	5	31	33 (3)			100 (2)	-
10	14	26			100 (8)	50 (6)	2.55
11	14	30		83 (12)	0 (2)		2.46
12	5	15	40 (2)		40 (2)	0 (1)	-
13	10	29	50 (4)	50 (4)	0 (2)		1.67
14	8	12		0 (2)		100 (6)	-
15	12	35	88 (8)		0 (4)		5.19*

Cats 1-3 were observed at Shotover Country Park, Oxford, cats 4-5 at Ryans Reserve, Kellerberrin, cats 6-10 on Rottnest Island, near Perth, cats 11-13 at North Head, Sydney, and cats 14-15 at Ethabuka, Queensland. Cats at each location were observed directly by day or at night under red or dim white light near settled areas, and were probably un-owned. χ^2 tests were not computed for cats observed <10 times; tests on cats 10, 11 and 15 used 1 df and were subjected to Yates' correction, whereas tests on other cats used 2 df. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Bold type indicates prey types that were hunted most efficiently.



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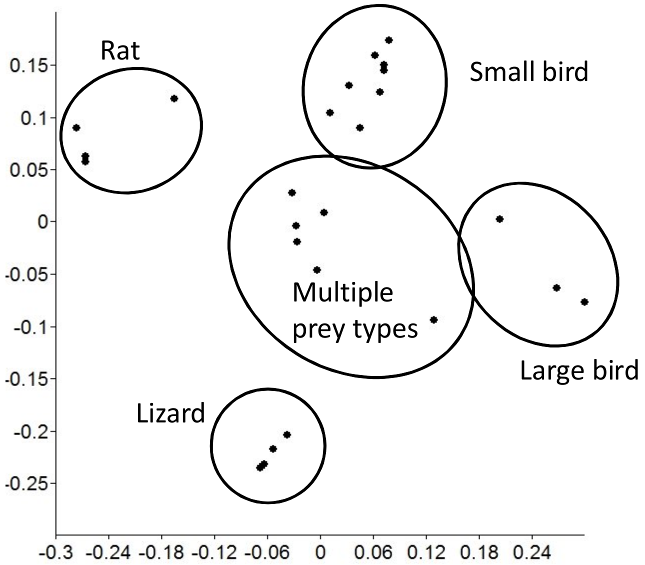

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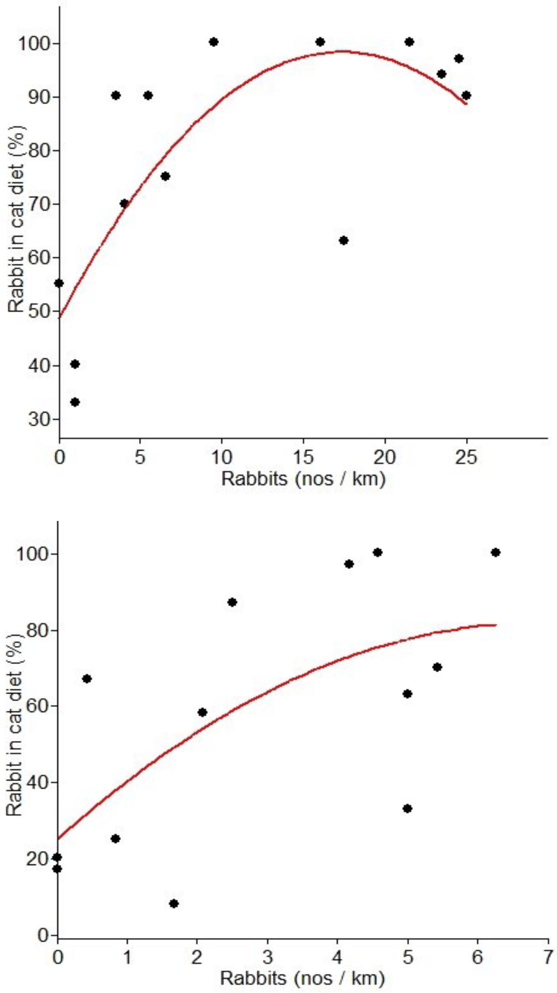

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