This is the peer reviewed version of the following article: Moseby, K.E., McGregor, H. and Read, J.L. (2020), The lethal 23%: predator demography influences predation risk for threatened prey. *Animal Conservation*, which has been published in final form at **https://doi.org/10.1111/acv.12623**.

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The lethal 23%: predator demography influences predation risk for threatened prey

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Running head: Predator demographics

Article Impact Statement

Predator demographics are an important determinant of predation impact and certain predator demographics should be targeted for protection of threatened prey

Key Words

Threatened species, predation, Australia, cat, body size, demography, diet, prey

Abstract

Globally, wildlife managers often control predator populations to protect biodiversity, livestock or other valued resources. Most assume that the predation impact of each individual predator is the same and that removing any individual predator produces a benefit to the target species. However, research suggests predation efficacy can vary within a predator species according to phenotypic characteristics. Understanding these individual differences may be critical for managing predation impacts on particular categories of prey including small populations where predation effects are amplified. We used dietary data from 1748 feral cats euthanased over 30 years during a control program in arid Australia to determine whether any predator attributes could predict their effect on different prey weight classes.

Feral cats in our study ate a wide range of prey including reptiles, mammals, birds and invertebrates. Demography (body mass) was a highly significant predictor of diet. Cats weighing 3 kg fed predominantly on prey < 50g increasing to > 500g when cats attained a body mass of 6 kg. Of more significance was that diet varied between demographic groups but also within a single demographic group (adult males) based on body mass, with results having significant implications for threatened prey. Modelling indicated that for a fixed predator population size, the predation rate on prey in a >500g weight class increased by 28% when the ratio of large (>4.2 kg) to small adult males varied according to its natural range (12-80% over the 30 year study). Results suggest that variations in predator demography can significantly impact predation rates on prey species and should be included in predator–prey models for small prey populations. On average, large male cats comprised 23% of the population and our findings suggest that targeting the “lethal demographic” and manipulating predator demography should be prioritised along with lowering predator density to reduce predation impacts.

Introduction

Introduced predators have caused the decline and extinction of hundreds of native species around the world. They have decimated native mammal populations in Australia (Burbidge and McKenzie 1989; Woinarski et al. 2012) and native birds in New Zealand, Japan, the United States and on islands (Arcilla et al. 2015, Young et al. 2013, Nogales et al. 2013). Furthermore, introduced predators have caused the failure of numerous global reintroduction programs through high levels of predation (Moseby et al. 2011; Clayton et al. 2014; Armstrong et al. 2006). Introduced predators are thought to exert a greater impact on prey than native predators due to the absence of shared evolutionary history (Saul & Jeschke 2015).

Introduced predators also have an impact on agriculture through predation on livestock (Greentree et al. 2000; McLeod et al. 2010). Due to the threats posed by introduced predators, their control is a common management action implemented for the protection of threatened species and livestock around the world (Courchamp et al. 2003; Burrows et al. 2003; Whitehead *et al*. 2010). The cost of these control programs can be high, for example Australia spends approximately 16 million dollars a year on the control of foxes for the protection of wildlife and domestic stock (McLeod 2004). Reducing the abundance of predators is the goal of most programs based on the assumption that predator abundance is the most important determinant of predation risk. This assumption is underpinned by the conceptual model of predator-prey dynamics stemming from the Lotka-Voltera model (Voltera 1926; Lotka 1932) that explains changes in prey abundance based on predator

67 abundance. A well-known example is the lynx-hare relationship where lynx populations
68 increase and decrease in synchrony but slightly lagging behind fluctuations in abundance of
69 snow-shoe hares (Keith *et al.* 1984). Hollings (1966) expanded predator-prey theory by
70 adding a functional response, arguing that the rate at which predators consume prey is a
71 function of their attack rate and processing time, which varies at different prey densities.
72 However, predator-prey models are based on assumptions, e.g. that the predator is
73 dependent on a single prey species, that the predator has a limitless appetite, and that a
74 fixed proportion of encounters leads to the death of the prey. These assumptions are rarely
75 met in the wild, impeding application of these models in conservation (Abrams 2007).
76
77 Importantly, most predator management programs and models of predator-prey dynamics
78 assume that each predator in the population has equivalent hunting efficacy (e.g. the
79 constant in Lotka's predator consumption rate or Hollings' predator attack rate). In the case
80 of vertebrates, this assumption is often violated because differences in the genetic make-
81 up, demography and life-time experience of predators influences individual's hunting
82 behaviour (McGregor et al 2014; Dickman & Newsome 2015; Moseby *et al.* 2015; Pettorelli
83 *et al.* 2015). For example, Austin *et al.* (2004) found significant intraspecific differences in
84 foraging behaviour in seals with likely resultant effects on predation models. In feral cats,
85 some individuals can learn to hunt vulnerable prey, leading to accelerated killings and
86 sometimes local extinction (Clout and Craig 1995; Moseby *et al.* 2015; Hardman *et al.* 2016).
87 Within small populations, such as threatened or reintroduced wildlife, predation effects are
88 amplified (Saul & Jeschke 2015) and intraspecific differences in predator attack rate or
89 preferred prey have the potential to drive catastrophic population declines. Thus, assuming

90 that all predators exert similar impacts on prey has the potential to incorrectly inform
91 management approaches (Pettorelli *et al.* 2015).
92
93 Some researchers have incorporated changes in predation rate into their models when
94 assessing predator impacts, for example, Nilson *et al.* (2005) incorporated the variation in
95 predation risk of young vs adult moose in predator-prey models of wolf impacts. However,
96 those studies that do focus on the variation in prey selection of predators tend to focus on
97 population changes such as seasonal (Davidson *et al.* 2013) or temporal changes in predator
98 diet or changes due to habitat structure (Hebblewhite *et al.* 2005), pack size (Packer *et al.*
99 1990, Loveridge *et al.* 2006) or prey breeding season (Davidson *et al.* 2013). Unfortunately,
100 the influence of individual predator traits on predation impacts has received less focus (but
101 see Funston & Mille 2006), despite studies reporting intraspecific differences in predation
102 impacts related to predator sex (Marlow *et al.* 2015), age (Litvaitis *et al.*, 1986), experience
103 (Estes *et al.* 2003) and body size (Moseby *et al.* 2015; Kutt 2012). Feline predators are
104 particularly flexible, exploitative and opportunistic, Cheetahs (*Acinonyx jubatus*) vary in prey
105 selection based on sex (Cooper *et al.* 2007), Lynx (*Lynx lynx)* on reproductive status (Pierce
106 *et al.* 2000), Cougars (*Puma concolor*) on age (Ross *et al.* 1997) and domestic cats (*Felis*
107 *catus*) on sex and body size (Kutt 2011; Moseby *et al.* 2015). Individual felines can also
108 specialise on certain prey based on individual experience and learn to hunt difficult prey
109 (Knopff & Boyce 2007; Dickman & Newsome 2015; Moseby *et al.* 2015).
110
111 Feral cats are an introduced species in Australia and predation by feral cats is listed as a Key
112 Threatening Process for more than 100 fauna species under the Commonwealth
113 Environment Protection and Biodiversity Conservation Act (1999). Most of these threatened

prey weigh between 35g and several kilograms. We used data from 1748 feral cats euthanased over 30 years during a predator control program in arid Australia to determine whether any predator attributes could predict their predation rate on fauna. We first determined whether the composition and diversity of feral cat diet varied amongst demographic groups and how this related to prey abundance and environmental variables. Secondly, we modelled the effects of different demographic ratios on the predation rates on populations of mammals >500g. This prey size is typical of many mammal species known to be threatened by feral cats and which have been subjected to high rates of decline and extinction in the study area (Moseby *et al*. 2011; Woinarski *et al*. 2012). We compared the potential impacts of various demographic combinations and used the results to determine if predation impacts can vary significantly even when predator and prey density remain constant.

Methods

Study area

This study was conducted in the vicinity of the Arid Recovery Reserve in the Roxby Downs region of northern South Australia (30 29'S, 136 53'E). The area is comprised of arid shrubland supporting longitudinal sand dunes overlying clay interdunal swales. The climate is arid with erratic annual rainfall averaging 166 mm (www.BOM.gov.au). The area supports multiple land uses including cattle grazing, mining and conservation. Feral cats are widespread throughout the region (Read and Bowen 2001) and live wild and independent of human contact (Moseby *et al.* 2009a*).*

Cat diet samples

Between January 1990 and January 2020, feral cats were removed from a 960,000 ha area in the Roxby Downs region through shooting, cage trapping and padded leghold trapping. Cats were removed principally as part of a local control program to reduce the pressure around the Arid Recovery Reserve (Moseby *et al.* 2011), but also as part of feral control on pastoral properties and around a mine.

For this analysis, we focused on feral cats, defined as those collected at least 3km from refuse dumps, residential or industrial areas. Cats were weighed, sexed and then dissected to examine stomach contents and to determine reproductive status of females. The lightest pregnant female cat was 2.3 kg, which was adopted as the minimum weight of both sexes at sexual maturity. This was slightly lower than the defined adult body mass of 2.5 kg recorded in other studies (Jones & Coman 1982; Brothers *et. al.* 1985). The coat colour of cats was recorded as either tabby, ginger, or black. Body condition was not included due to inconsistencies with field scoring methods. Stomach contents were examined for prey items and where possible each item was identified to species level. Invertebrate species were identified to Order. A comprehensive 20 year inventory of prey species from the local area was used as a guide (Read 1998; Read *et al.* 2000; Read & Cunningham 2010; Moseby *et al.* 2009b).

Cat and Rabbit density

The density of feral cats and one of their key prey items, the European rabbit (*Orytolagus cuniculus*) was estimated using two 20km spotlight transects conducted in the study area every two months from April 1989 until 2013 and then less frequently for the duration of the study (see Read and Bowen 2001 for methods). Results were averaged across quarters

and if no transects were conducted within a quarter, then the previous quarter's estimate was used.

Variables influencing Diet

We divided prey into six prey groups; invertebrates, birds, herpetofauna (reptiles and frogs), rabbits, small mammals (<20g) and rodents 20 – 60g (comprising the spinifex hopping mouse (*Notomys alexis)* and nationally threatened plains mouse (*Pseudomys australis)*). Carrion was not considered as it was recorded in <2% of samples. We used a count of each prey group per stomach, with the exception of rabbits and birds which were considered as binary variables (present/absent) as they were almost exclusively recorded as single prey items.

First, we explored data for simple relationships between cat weight and prey size. The average live weight of each prey species was derived from trapping and shooting studies at the study site (Read 1998; Read 1999; Read & Cunningham 2010; Moseby *et al.* 2009b). We then averaged the live weight of all the prey items found within each cat stomach, then ran a Generalised Linear Model (R, v3.5.1, www.r-project.org) with a negative binomial distribution against cat weight, and compared this to a null model using an information theory framework ie we considered a model with an Akaike weight > 0.5 and delta AICc > 4 having relatively better support compared to the null models (Burnham and Anderson 1998). r

Next, for each prey group, we compared their abundance in each cat's stomach with a range of individual cat characteristics and extrinsic variables. For prey categories using count data we used two-stage hurdle generalised linear models (Potts and Elith 2006; Zuur *et al.* 2009), as data were over-dispersed and contained many zeros. These two-stage models ran a

184 binary logit model in tandem with a truncated negative binomial model fitted only to counts
185 greater than 0. The former models the probability of eating a prey species, the latter models
186 the probability of how many are eaten. For rabbits and birds (binary variables), we applied
187 generalised linear models with a binomial distribution.

188 The explanatory variables used in each prey group model of cat diet included cat weight
189 (both a linear and parabolic relationship peaking at 3 kg used in separate models), sex,
190 pelage (ginger, tabby, black), rainfall recorded in the last 12 months, either maximum
191 nightly temperature (for birds and herpetofauna only, as this would affect activity) or
192 maximum temperature averaged over each month (as more representative of climatic
193 conditions), and method of sampling (shot or trapped). Rainfall and temperature data were
194 sourced from the Bureau of Meteorology (www.BOM.gov.au) from the closest registered
195 recording location (Olympic Dam Aerodrome, within 80 km of each sample). Rabbit density
196 was also included in the models and abundance of medium sized rodents (20-60g) was
197 included as a categorical variable on a scale of 0-5 (0=absent, 5=highest abundance). This
198 index was used instead of trapping rates as sampling was not consistent between habitats
199 and time periods. Capture rates of rodents in the weight range 20-60g fluctuated from 0 to
200 10%, and were allocated scores ranging from 1-5 (Read 1994; Moseby & Read 2001; Moseby
201 *et al.* 2009; Arid Recovery unpublished data).

202 As prey consumption of certain groups could be affected by dietary preference, we also
203 added a variable 'preferred food' into the model. This variable quantified the number of
204 prey items present in each cat's stomach that were from a more preferred prey group. We
205 ranked prey groups based on preferences found in existing literature (Paltridge *et al.* 1997,
206 2002; Pavey *et al.* 2008; Spencer *et al.* 2014; Read *et al.* 2019; Kutt 2012), then for each prey

group we added the number of all of the more preferred prey items in each cat stomach as a variable. We ranked preferred prey highest to lowest; rodents 20 – 60g; rabbits, small mammals (<20g), birds, herpetofauna, then invertebrates.

For the prey models using bird and rabbit prey groups, we included an interaction term between cat weight and average monthly temperature, as birds and rabbits are most likely to have young from Winter to Spring (Read *et al.* 2000; Bowen & Read 1998) which could be targeted by smaller cats.

For each of the six prey groups, we ran independent analyses to determine the best model for predicting their presence or count in cat stomachs using information theory, based on Akaike Information Criterion (AIC) weights. We used AIC instead of AICc, as our sample size divided by candidate variables was always greater than 200 (Burham & Anderson 1998). As we considered all variables possible important predictors of cat diet, we ran 12 models with different combinations of biologically plausible variables, where each variable was present within 4-6 models. A global and null model was also added to each model set. The sampling method (trapped vs shot) was included in all models bar the null, as trapped cats were less likely to have eaten in the previous 12 hours than shot cats. We then looked at model averaged coefficients, and added another model containing only variables with > 73% relative importance, suggesting an AIC delta difference of 2 or less (Richards 2005). For each analysis, we considered the model with the most support to be the model with a delta of 0 if >2 difference.

Once we had selected the models with the most support, we investigated model fit and predictive power using quartile-residual plots for all models, rootograms for zero-inflated

hurdle models (Kleiber & Zeileis 2016) and receiver operator curves for the Area Under Curves (AUC) for binomial models.

The influence of demography on kill rates of different prey groups

We tested whether the proportion of large males in the population would change predation pressure on the rabbit prey category at a population level, when all other variables were taken into consideration. The topprey group models were used to simulate the stomach contents of 100 random cats each day for 365 days given a range of realistic demographic and environmental variables. We used an input of temperatures based on long term daily averages obtained from the study area and we simulated an entire year. We used a demographic ratio of male:female:subadult of 2:2:1 based on the long term average from shot cats in the study area and yearly rainfall was taken from a normal distribution from the site. The index of rodents 20-60g was a uniformly drawn random number between 1 and 5. As some prey group outcomes are influenced by others, we included any of our significant prey preference hierarchies in the models. We assumed each stomach content would represent 10 hours of hunting; the time taken for 95% of small and large food items to transit the stomach of owned cats (Chandler *et al.* 1997).

We reran the model simulation 100 times using different ratios of adult males that were either small (the first and second quartile of adult male's cat body mass in the population, 2.3-4.2 kg) or large (third and fourth quartile 4.3 kg-6 kg). Female weight ratios were not included due to the small proportion of females weighing over 4.2kg. In every model, we assumed the same feral cat population size and that rabbit density was moderate and stable (40 km^{-2}, the average from 2009-2019). We then ran a generalised linear model where each

252 datapoint was one of the 100 simulations of the relationship between large:small male
253 ratio, and predicted annual rabbit kill.

254 To investigate whether the percentage of large adult male cats in a population was related
255 to density, for each year we summed cat density and portion of large adult males in the
256 sampled population and ran Generalised Linear Model (R, v3.5.1, www.r-project.org)
257 comparing large males against estimated cat density, then compared this to a null model
258 using an information theory framework ie we considered a model with an Akaike weight >
259 0.5 and delta AICc > 4 as having relatively stronger support compared to the null models
260 (Burnham and Anderson 1998).

261 **Results**

262 There were 3025 recorded cats euthanased in the study region between January 1990 and
263 January 2020. Of those, 1748 were caught away from human habitation and had a full suite
264 of demographic and stomach data. For these cats, 1288 were shot and 460 were trapped in
265 leghold (>95%) or cage traps. Adult female cats (average weight=3.33, SE=0.02) were
266 typically smaller than adult male cats (average weight=4.19, SE=0.03, Fig 1). The
267 demographic ratio averaged across all years between male:female:subadult was 2.6 : 2.4 : 1,
268 but ranged from 15 : 13 : 1 to 1.1 : 0.8 : 1. For adult male cats the percentage of large cats in
269 the population each year varied from 12% to 80% (average= 45%). Demography varied
270 independently of density, as a model of cat density against the percentage of large adult
271 male cats had less support than a null model (AICc of model compared to null: loglik 26.7 vs
272 26.6, AICc -46.5 vs -48.6, delta 2.3 vs 0, weight =0.2 vs 0.8).

273 *Diet vs demography*

There were 75 different vertebrate species recorded in the diet, and 12 invertebrate families. When the size of cats was compared with their stomach contents, subadult cats less than 2.3 kg predominantly ate food items less than 10g in weight such as invertebrates, small mammals and reptiles, but as cats increased in size, so too did their intake of larger food sources (Fig. 2). Once cats attained a body mass of more than 4 kg their average weight of dietary items increased markedly (Fig.2). Larger cats over 5.5 kg predominantly ate prey greater than 500g, especially rabbits. The average weight of all prey species in a cat's stomach increased on a log scale with cat weight (Fig 3, AIC of model compared to null: loglik -3412 vs 3513, delta 0 vs 200, weight =1 vs 0). Dietary diversity within stomachs of each cat size declined with cat weight (AIC of model compared to null: loglik -2790 vs 5584, delta 0 vs 9, weight =0.99 vs 0.1), with stomachs from larger cats containing fewer dietary categories than smaller cats (-0.05/kg, $z=3.3$, $P<0.001$).

When models were run comparing stomach contents with individual cat attributes and environmental variables, methodological and environmental variables were prominent in nearly all top ranking models (Table 1). For each prey category, the most parsimonious model was selected with a substantial margin over other candidate models (Akaike weight > 0.95, and delta > 2 of next strongest model, see Suppl Material 1). Most variables within each model had a high relative importance (>0.95) and were significant, except for certain interaction terms. All hurdle models had stable rootograms and QQ plots (see Suppl Material 2), all binomial models had strong predictive power (rabbit AUC = 0.79, birds = 0.62).

Cats that were trapped were around 50% less likely to have prey present for all groups than shot cats. In hotter temperatures, cats ate fewer rabbit and birds, yet more small mammals,

297 herpetofauna and invertebrates (Table 1). We found no difference in diet between cats of
298 different pelage colouration. Interestingly, for a given weight class, female cats were slightly
299 more likely to eat rabbits than males. If cats had already eaten more preferred prey, they
300 were less likely to eat rabbit or small mammals, however, no relationship was found for
301 birds and herpetofauna, and a positive association with invertebrates (Table 1).

302 Cat weight was of high relative importance in the highest ranking models for all prey groups
303 except birds. Rabbits became more prevalent in stomachs of cats of larger sizes (Fig. 4), with
304 an interaction with average monthly maximum temperature (Table 1). Smaller cats were
305 more likely to eat rabbit during cooler months (Fig. 5) whereas larger cats ate rabbits
306 regardless of temperature. Invertebrates and herpetofauna were predominantly eaten by
307 smaller cats, whilst rodents 20-60g displayed an approximately parabolic relationship (Fig.
308 4).

309 **Using models to predict rabbit kill rates under different demographics**

310 There was a strong significant relationship between the ratio of large to small adult male
311 cats and rabbit consumption compared to the null model (loglik = -895.7 vs -906.7, delta = 0
312 vs 20, weight = 1 vs 0, coef=34, se=7, R^2 = 0.19 F = 24.3 1 on 98 DF, P < 0.001***). The
313 greater the ratio of large to small male cats in the population the higher the predation
314 impact would be on rabbits (Fig.6). For a random population of 100 cats, every 10%
315 increase in the proportion of the male population over 4.2g would result in an additional
316 340 extra rabbits per year being killed. The actual proportion of large to small adult cats
317 varied from 13 to 80% over the study period.

318

Discussion

The significant influence of cat body mass on predation of different prey groups suggests that individuals within a population can disproportionately affect prey populations. This result has implications for managing the undesired impacts of predators including high predation rates of introduced predators on threatened species. The recorded ratios of large to small adult male cats over our 30 year study ranged from 13% to 80% demonstrating that demographic ratios vary significantly in the wild even within demographic groups. We found that for a predator and prey population of a fixed size, the predation rate on prey >500g increased by 28% when comparing the lowest and highest ratios recorded during our study. Our results support other studies that have found differences in predation rates based on body size both within a species (see Pettorelli *et al.* 2015 for review, Kutt 2012) and between species (Carbone *et al.* 1999; Vezina 1985). However, our results contrast with the results of a more limited study by Yip *et al.* (2014) who found no relationship between the types of prey consumed and cat size.

Results suggest that targeted control of individual predators within certain demographic groups may significantly improve management outcomes depending on the size of prey being protected. When modelling the impacts of predators on threatened or small prey populations, the proportion of predators in each adult size category may need to be explicitly included in predator prey models. Unfortunately, most predator prey models use population means and consider predators to be identical individuals (e.g. Fryxell *et al.* 2007; Nilsen *et al.* 2005; Post *et al.* 1999; Stenseth *et al.* 1997; Vucetich *et al.* 2005, 2011). Some

342 researchers have included sex or age class in predator prey models to improve their
343 predictive power e.g. Nilsen *et al.* (2007) but in general, individual traits are rarely
344 considered (Pettorelli *et al.* 2011). This can have significant implications for developing
345 appropriate management strategies for threatened prey populations where intraspecific
346 differences in hunting behaviour are likely to have amplified effects.
347
348 Our study is significant as, whilst previous studies have shown differences in predation rates
349 between sub-adults and adults within a population, we have shown that even changes
350 within a single demographic group (adult male cats) are likely to affect predation rates.
351 Although this has implications for the control of introduced predators for the protection of
352 threatened species, our results have broader implications including for practitioners
353 protecting native prey or livestock from native or exotic predators. Understanding how
354 predation rates change with demography can assist managers with developing more
355 targeted control methods, improving cost effectiveness and efficacy. In our study, prey
356 weighing over 500g were more likely to be eaten by cats over 4.2 kg in body mass. The
357 proportion of cats in this size category averaged 23% of the population each year but ranged
358 from 7% to 45% over the 30 year study period. This lethal 23% is supported by other field
359 studies that have shown male (Marlow *et al.* 2015), large 4 kg males (Moseby *et al.* 2015) or
360 individual cats (Hardman *et al.* 2016) can have catastrophic impacts on threatened species
361 populations. Targeting this 'lethal demographic' would increase the efficacy of predator
362 control for protection of threatened species that have a body mass of more than 500 g and
363 may explain why some control programs that record a decline in predator density are
364 unable to demonstrate a resultant increase in threatened species abundance (Walsh et al.
365 2012).

Studies have recorded feral cats preying on species as large as 220-280g (Dickman 1996; Yip et al. 2014), up to their own body weight (Paltridge *et al.* 1997) and consuming mammals weighing 1.6 kg (Marlow *et al.* 2015), 2 kg (Moseby *et al.* 2015; Hardman *et al.* 2016) and even 4 kg (Read *et al.* 2019). Our finding suggests that the preferred prey weight of 40g or less determined by Pearre and Maass (1998) for *Felis catus* globally is too simplistic and that feral cats may be a significant threat to species up to several kilograms in body mass.

The interacting effects of cat size, prey availability, prey preferences, rainfall and season on cat diet supports other studies that suggests predation impacts are complex and depend on a range of intrinsic and extrinsic factors (Pettorelli *et al.* 2011). Some studies have found that larger predator species consume a higher diversity of prey than smaller ones (Radloff and du Toit 2004; Schoener 1969). This relationship has also been demonstrated within the same species (Yip *et al.* 2014) which, in sexually dimorphic species, is thought to be a response to the higher protein requirements of larger males (Nagy 1987). However, we found large cats to have lower diversity diets. Part of this reduction in diversity may be an artefact caused by the local extinction of many mammals >100g from the study area (Moseby *et al.* 2011) limiting the availability of larger prey. However, reptiles weighing up to 450 g were included in the diet of cats and were present in the study area (Read 1994). Single prey species are thought to only form the bulk of the diet of individual cats that have developed specialist hunting methods (Dickman 2009 but see Dickman and Newsome 2015) or where prey are very abundant and easy to hunt (Fitzgerald and Turner 2000; Yip *et al.* 2014; Denny and Dickman 2010). However, our results suggest that specialisation may occur when cats attain a body size where they can improve their hunting efficiency by selecting

389 and targeting larger prey, rendering these cats particularly destructive in wildlife protection
390 programs.

391

392 Sex is another phenotypic characteristic that has been shown to affect individual predation
393 rates in weasels (*Mustela nivalis)* (Sundell, 2003), Cheetahs (*Acinonyx jubatus*) (Cooper *et al.*
394 2007) and wolf spiders (*Pardosa vancouveri*) (Hardman & Turnbull 1974). However, sex only
395 weakly influenced rabbit consumption when body mass was held constant. Breeding female
396 cats may be targeting young rabbits which emerge most often in Winter and Spring (Bowen
397 & Read 1998). Juvenile rabbits may be easier for smaller non-breeding female cats and/or
398 younger inexperienced cats to hunt. This is supported by the highly significant interaction
399 between weight and temperature for rabbit consumption with smaller cats feeding on
400 rabbits in the cooler months and larger cats feeding on rabbits regardless of temperature.

401 Although male cats generally attain a larger body mass than females it appears to be size
402 rather than sex per se that drives differences in prey consumption. Studies that have found
403 male cats to specialise on threatened prey species and cause significant predation impacts
404 (Marlow *et al.* 2015) are likely recording a size rather than a sex effect (Moseby *et al.* 2015).
405 However, the influence of body size could not be effectively separated from age. Heavier
406 cats are likely to be older but the absence of a reliable ageing mechanism for feral cats
407 makes it difficult to separate out the two demographic effects. Age is an important
408 determinant of predation rate in other feline species but usually these studies compare
409 subadult with adult animals (Litvaitis *et al.* 1986; Knopff *et al.* 2010). We considered
410 subadults separately from adult cats in an attempt to separate age from size effects and,
411 like other felid studies, found young cats more likely to consume invertebrate and smaller

412 prey items than adult cats. However, whether this result is simply due to smaller body size
413 or is in fact related to age effects such as lack of experience or shyness is unknown.
414
415 The presence of 20-60g rodents at a site may provide some protection for other mammals.
416 Small mammal and rabbit presence in cat stomachs were lower if 20-60g rodents were
417 present, suggesting that when rodent abundance is high, cats will preferentially eat rodents.
418 This protection may be most pronounced during wet years as higher rainfall in the previous
419 12 months increased the incidence of 20-60g rodents in the diet probably due to rainfall-
420 induced resource pulses leading to localised rodent population booms (Brandle & Moseby
421 1999; Letnic et al. 2005). Alternatively, this protection may be unsustainable: when rodent
422 numbers crash during droughts, cats may prey switch to other fauna (Courchamp et al 2000;
423 Read and Bowen 2001).
424 Our findings have significant implications for conservation of small populations of
425 threatened species where predation is a major threat. Controlling the “lethal demographic”
426 is likely to be just as important as reducing the density of introduced predators per se.
427 Predator control methods that remove large cats over 4 kg are likely to yield significantly
428 greater conservation benefits to prey weighing more than 500g than removing random cats
429 from the population. When reintroducing or protecting threatened species of this size,
430 practitioners could target cats that prey on these species through the use of toxic implants
431 in prey species (Read *et al.* 2015), audio lures that include female mating calls and olfactory
432 lures that are attractive to male cats. Control methods that are likely to target small cats,
433 young cats or inexperienced hunters, such as cage traps and control methods that use food
434 based lures (Short *et al.* 2002), should be used sparingly.

435

436 Our results reveal that accounting for individual variability in predation impacts may help
437 resolve the discrepancy between patterns predicted in theoretical versus wild populations
438 and provide more accurate models for predicting predation impacts on threatened prey
439 populations. We urge global conservation managers and researchers to measure individual
440 differences in predation rates of threatened prey by other predator species and incorporate
441 this knowledge into prioritising on ground management actions that target predators with
442 'lethal demographics'.

443

444 **Acknowledgments**

445

446 We wish to thank all those involved in collecting and processing the specimens over the 30
447 year study particularly K Lamb, P Paisley, T. Gotch, C McGoldrick, M Young, J Crompton, F
448 Bernhardt and J Millard. Arid Recovery, WMC Resources and BHP staff all contributed to
449 maintaining the long term dataset. K. Kovac kindly assisted with designing the database and
450 J Potts provided statistical advice. This study was conducted under Animal Ethics Permit
451 8/2017 from the Wildlife Ethics Committee.

452

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754

755 Table 1. Details of variables within models with the strongest support for each prey group
756 predicted within cat stomachs. 'Type' refers to type of model. If modelling a count, two-
757 stage hurdle models were used with a zero and count, while binary models used a binomial
758 'GLMuhi'. The variable pelage was also modelled, but not present in any top ranked model.

Prey category	Type	Variable details	AIC relative importance	Model averaged coefficient	SE	Z	P
Rodents 20-60g	Zero	Intercept		-3.46	0.21	16.33	<0.001
		Sample method- trapped	0.95	-0.37	0.15	-2.45	0.014
		Cat weight (parabolic)	1	-0.61	0.11	-5.41	<0.001
		Rodent abundance index (0-5)	1	0.87	0.05	16.05	<0.001
	count	Intercept		-0.73	0.34	-2.14	0.032
		Abundance index (0-5)	1	0.23	0.07	3.42	<0.001
		Sample method- trapped	0.95	-0.45	0.18	-2.53	0.011
Rabbits	binomial	Intercept		1.35	0.92	1.48	0.14
		Sample method- trapped	1	-0.64	0.14	-4.45	<0.001
		Preferred food	1	-0.56	0.12	-4.78	<0.001
		Cat weight (linear)	0.95	-0.06	0.23	-0.26	0.792
		Average month temp. (°C)	1	-0.11	0.03	-3.74	<0.001
		Rabbit density	1	0.45	0.21	2.2	0.028
		Rainfall in last 12 months	0.97	-0.37	0.1	-3.74	<0.001
		Sex- Male	0.95	-0.23	0.13	-1.73	0.084
		Weight (linear) × av. month temp. (°C)	0.97	0.02	0.01	2.57	0.01
Small mammals	Zero	Intercept		-1.68	0.4	-4.16	<0.001

		Sample method- trapped	1	-0.87	0.14	-6.18	<0.001
		Rain in last 12 months	1	0.47	0.09	5.48	<0.001
		Cat weight (linear)	1	-0.15	0.05	-3.23	0.001
		Preferred food	0.97	-0.15	0.06	-2.58	0.01
		Average month temp. (°C)	0.95	0.02	0.01	2.63	0.009
	Count	Intercept	0.95	-2.66	2.44	-1.09	0.277
		Rain in last 12 months	0.95	0.29	0.13	2.23	0.026
Birds	Binomial	Intercept		-0.64	0.37	-1.72	0.085
		Sample method -trapped	1	-0.9	0.24	-3.69	<0.001
		Average monthly temp. (°C)	1	-0.05	0.01	-4.09	<0.001
Herpetofauna	Zero	Intercept		-1.7	0.32	-5.37	<0.001
		Sample method-trapped	1	-1.43	0.17	-8.36	<0.001
		Maximum daily temperature	1	0.04	0.01	5.58	<0.001
		Cat weight (linear)	1	-0.12	0.05	-2.51	0.012
	Count	Intercept		-8.8	52.57	-0.17	0.867
		Sample method- trapped	1	-1.03	0.35	-2.98	0.003
Invertebrates	Zero	Intercept	1	-2.81	0.49	-5.78	<0.001
		Sample method- trapped	1	-0.51	0.16	-3.19	0.001
		Cat weight (linear)	1	-0.36	0.06	-6.43	<0.001
		Rain in last 12 months	1	-0.22	0.1	-2.11	0.035
		Preferred food	1	0.14	0.03	5.05	<0.001
		Average month temp. (°C)	1	0.09	0.01	8.52	<0.001
	Count	Intercept		-8.72	53.01	-0.16	0.869
		Sample method- trapped	1	-1	0.28	-3.55	<0.001
		Cat weight (linear)	1	-0.44	0.1	-4.38	<0.001
		Preferred food	1	0.11	0.06	1.97	0.049

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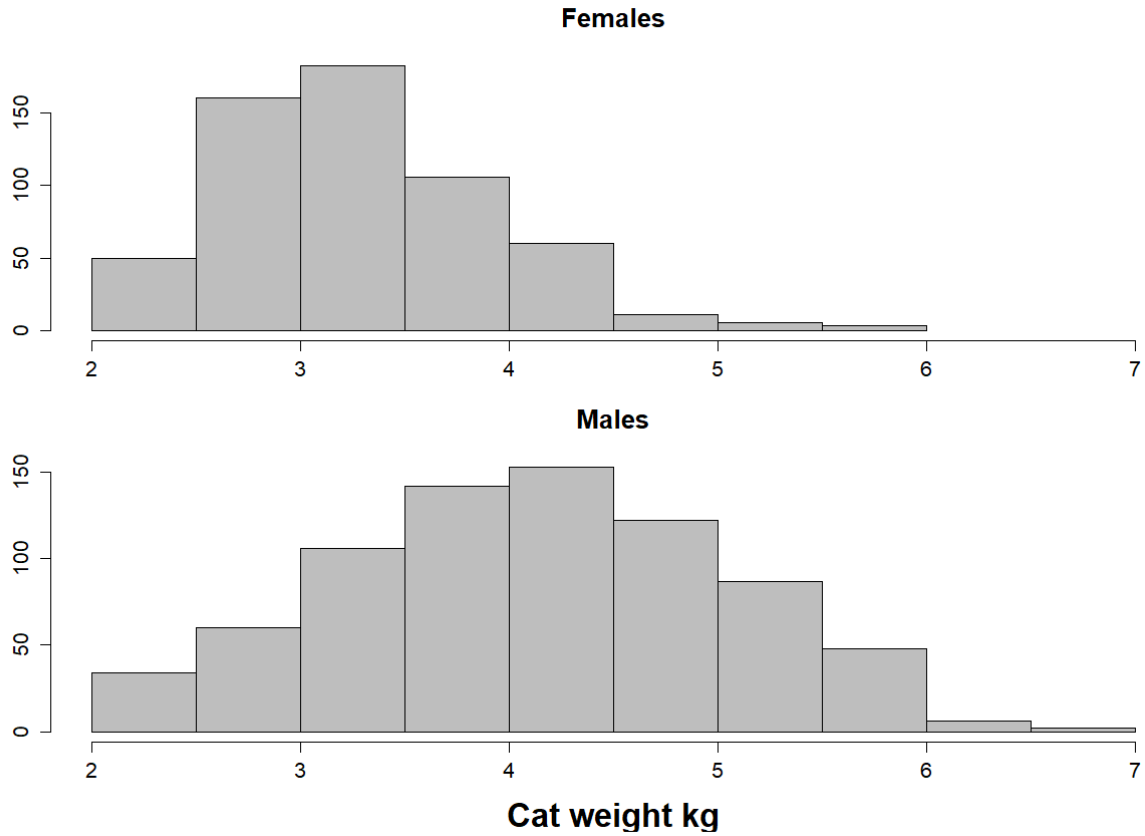
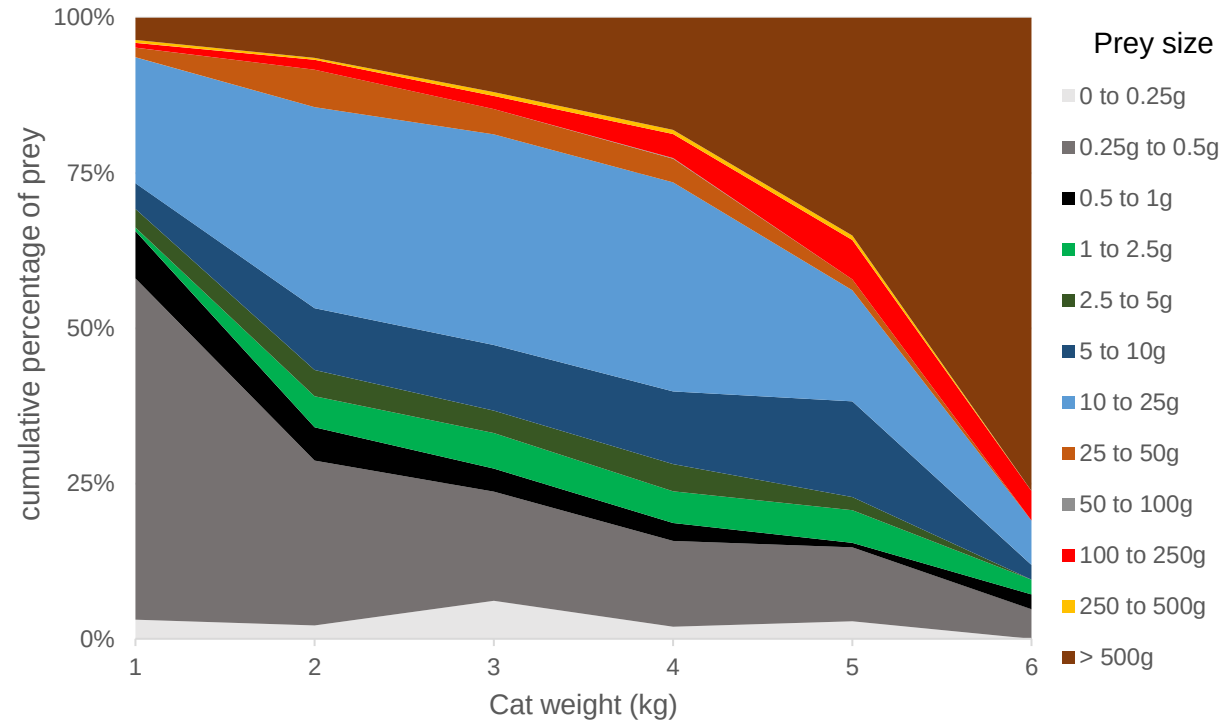


763

764 Fig 1. Histogram of the spread of weights of adult female and male cats sampled during the

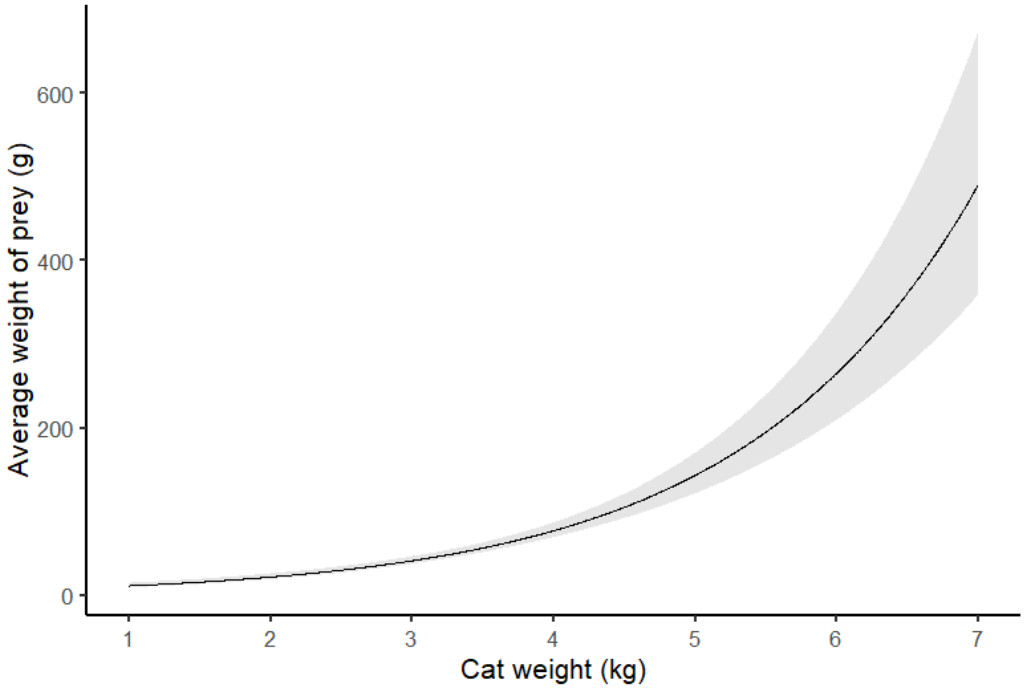
765 study.

766



767

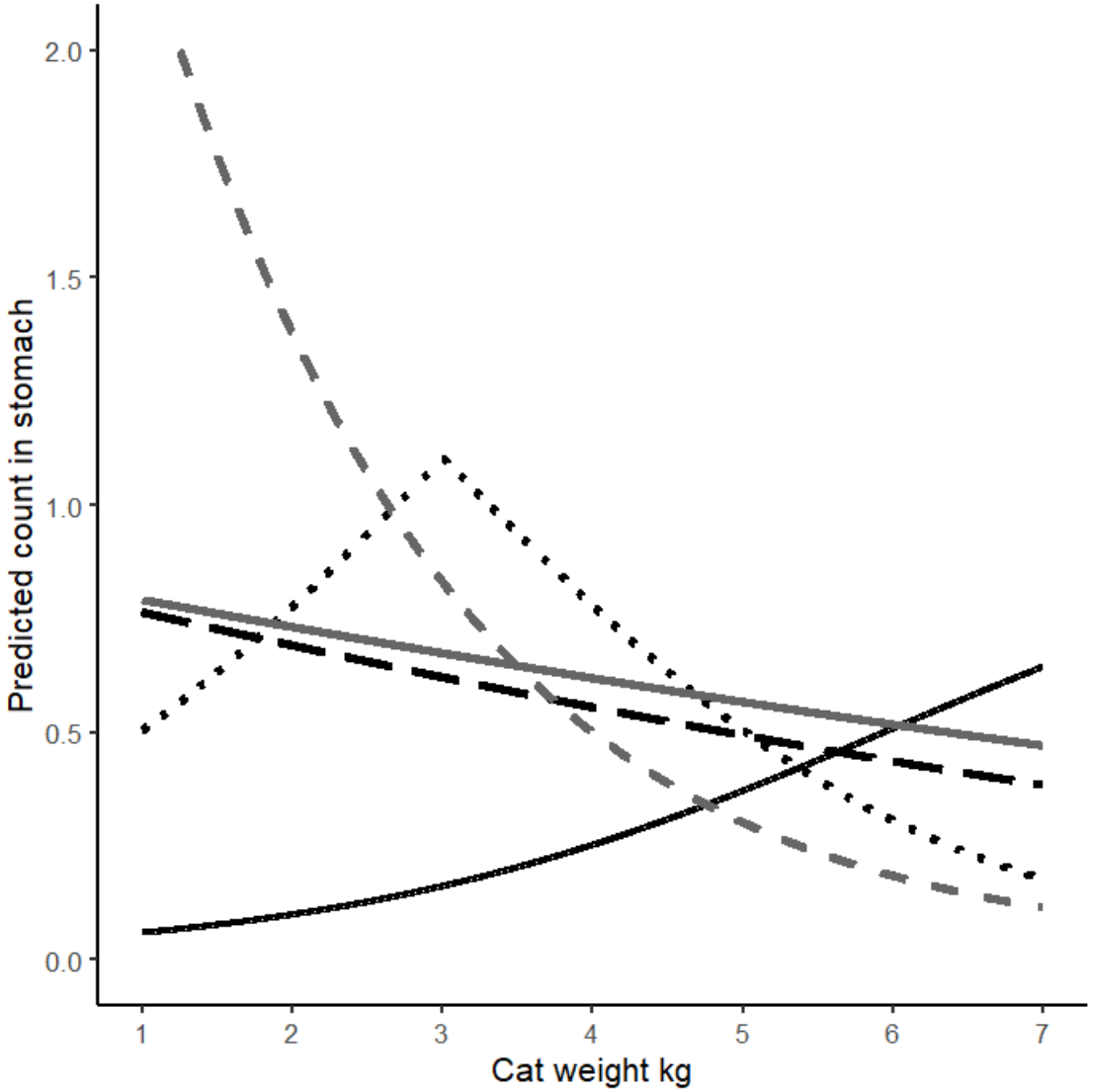
768 Figure 2. Distribution of prey size found inside cat stomachs for cats in each cat weight class.



769

770 Figure 3: Model predictions of the relationship between cat weight and average weight of all

771 prey species found in each stomach, including 95% confidence interval (grey shading).



772

773 Figure 4: Predicted relationships between cat weight and prey categories found in cat
774 stomachs from models with the strongest support for the five prey categories; rodents 20-
775 60g (dots), rabbits (solid black), small mammals <20g (black dash), herpetofauna (solid grey)
776 and invertebrates (grey dash). All other variables were set as constant.

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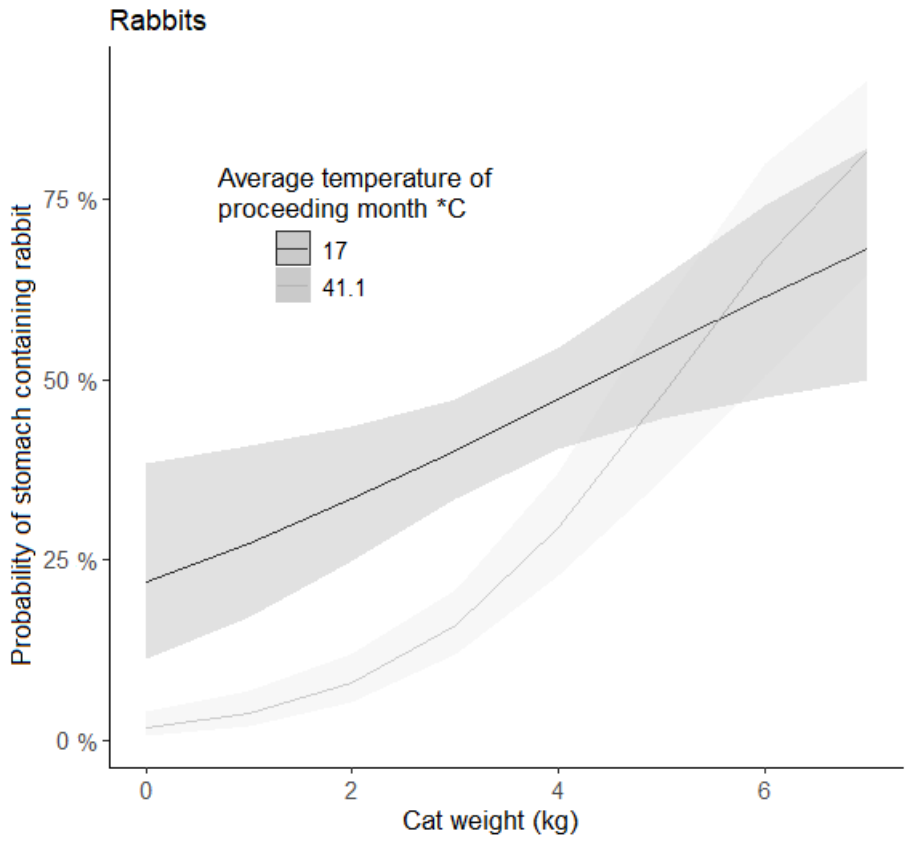


781

782 Figure 5: The probability of a cat stomach containing rabbit in relation to cat weight during

783 the hottest months (pale grey) and coldest months (dark grey) at the study site.

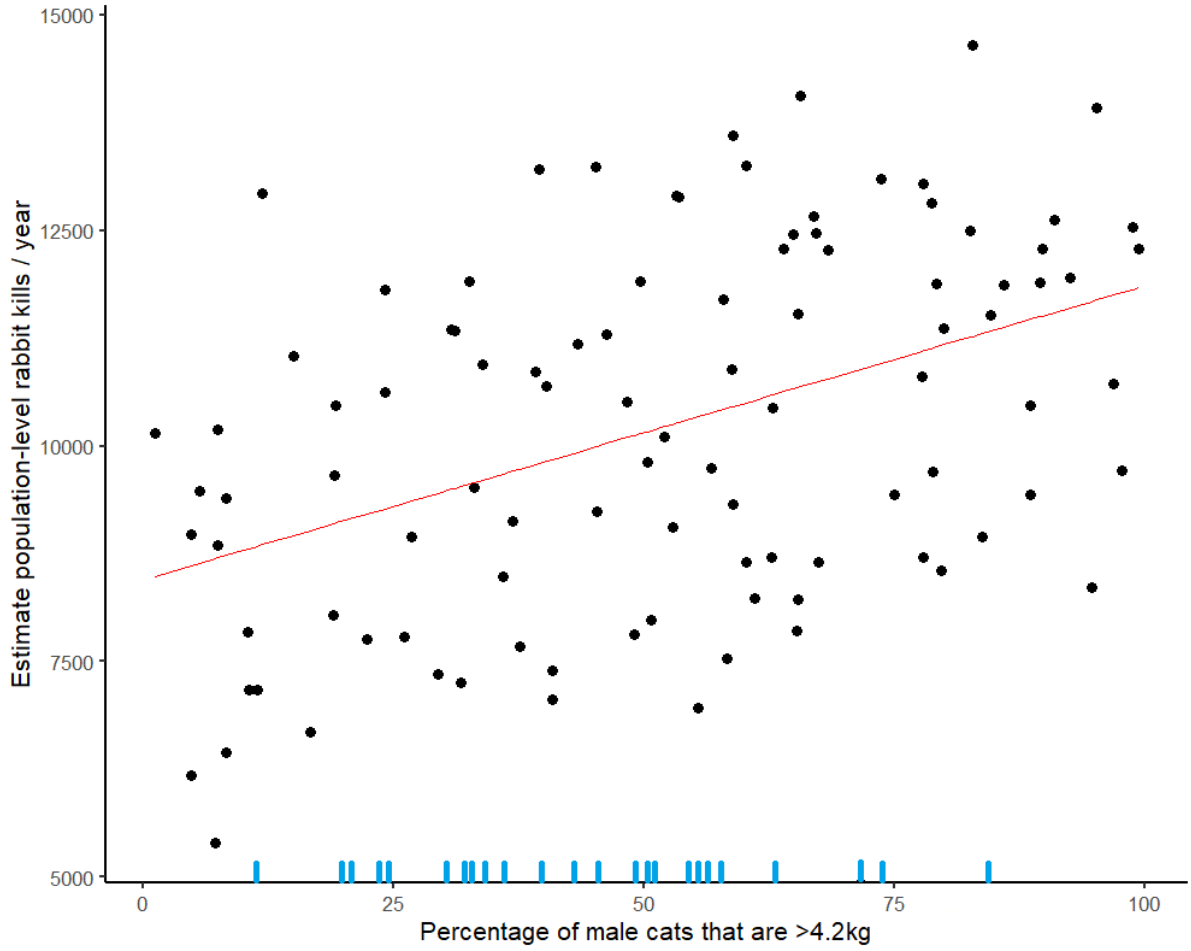


Figure 6. Estimated annual kill rate of rabbits in 100 simulated populations of feral cats, comparing scenarios with varying percentage of the male feral cats >4.2 kg. Constants in all scenarios is cat population size (100 cats), a 2:2:1 ratio of male:female:subadult and rabbit density of 40km^{-2}. The variables of rainfall, temperature and number of rodents 20-60g were drawn from a random sample according to real patterns around the study area. Blue tick marks indicate natural spread of the percentage of males >4.2 kg sampled from the study area in the years between 1990 and 2019.

795 Supplementary Material 1. Results from model selection tables comparing variables
796 affecting prey groups in cat stomachs, using AIC values (see Table 1). Only the top model,
797 second best model, global model and null model are presented for brevity.

Prey Group	Model details	df	LogLik	AIC	Delta	Weight
Rodents 20-60g						
	Top model	8	-1067	2150.1	0	0.78
	Second model (global)	12	-1064.5	2153.2	3.1	0.16
	Null	3	-1264.5	2534.9	384.8	0
Rabbits						
	Top model	9	-903.4	1825	0	0.81
	Second model (global)	11	-903.1	1828.3	3.3	0.15
	Null	1	-1046.3	2094.6	269.6	0
Small mammals						
	Top model	9	-1633.4	3284.8	0	0.75
	Second model (global)	12	-1631.5	3287.3	2.4	0.22
	Null	3	-1685.9	3377.9	93.1	0
Birds						
	Top model	3	-500.3	1006.6	0	0.46
	Second model	7	-497.6	1009.2	2.5	0.13

	global model	10	-496.1	1012.4	5.7	0.03
	Null	1	-516.4	1034.9	28.2	0
Herpetofauna						
	Top model	7	-1504.8	3023.7	0	0.83
	Second model	6	-1508	3028	4.3	0.1
	global model	10	-1507.3	3034.7	11	0
	Null	3	-1575.7	3157.4	133.8	0
Insects						
	Top model	11	-1459.8	2941.8	0	0.62
	Second model (global)	12	-1459.3	2942.8	1	0.38
	Null	3	-1581.4	3168.9	227.1	0

798

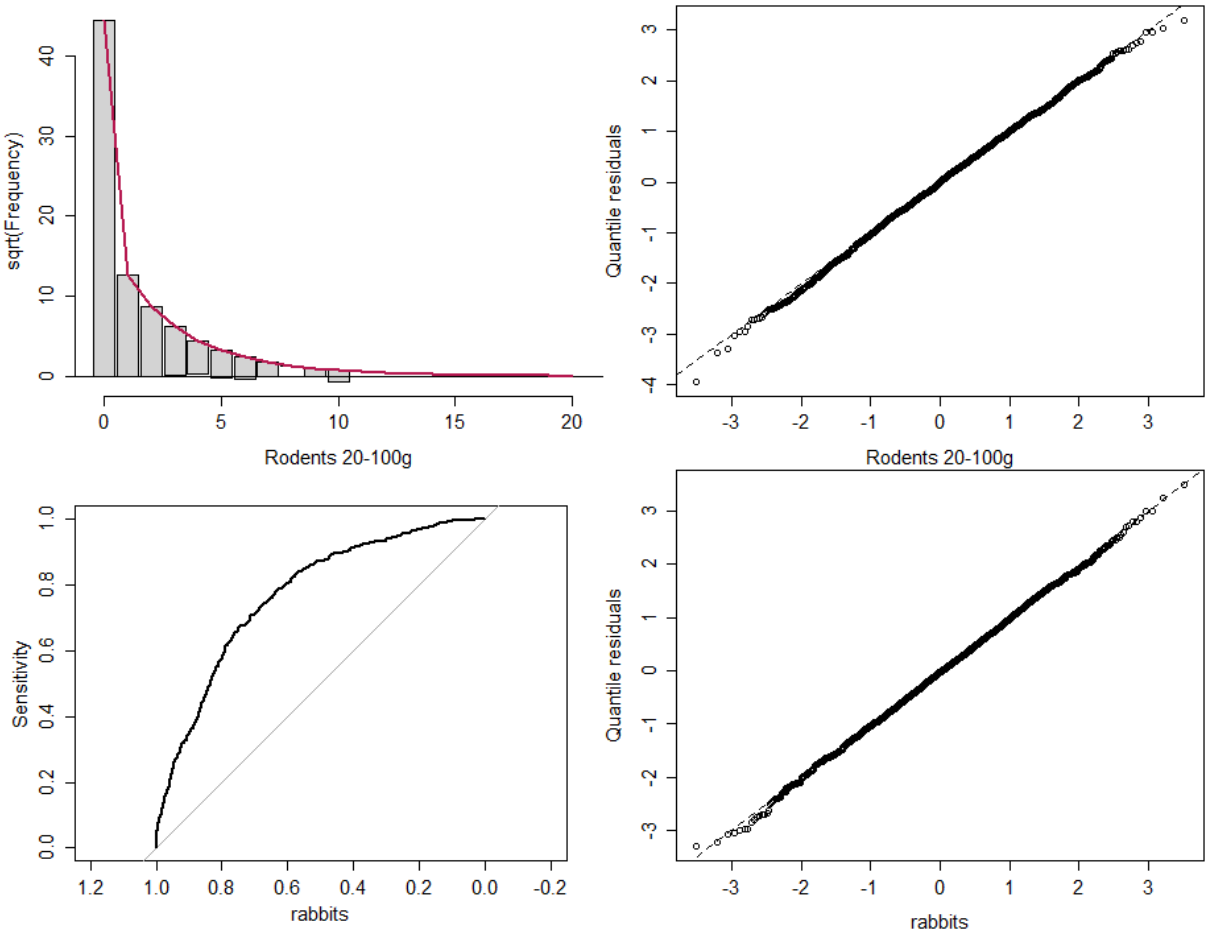
799 Supplementary Material 2. Model performance diagnostics for the top models of the

800 (Supplementary Material 1) likelihood of certain prey groups being recorded in feral cat stomachs.

801 For two-stage hurdle models of count data, we present rootograms and QQ residual plots (rodents

802 20-60g, reptiles, small mammals <20g, insects). For binary models of presence-absence (Rabbits and

803 birds), we present Area Under Curves (AUC) plots and QQ residual plots



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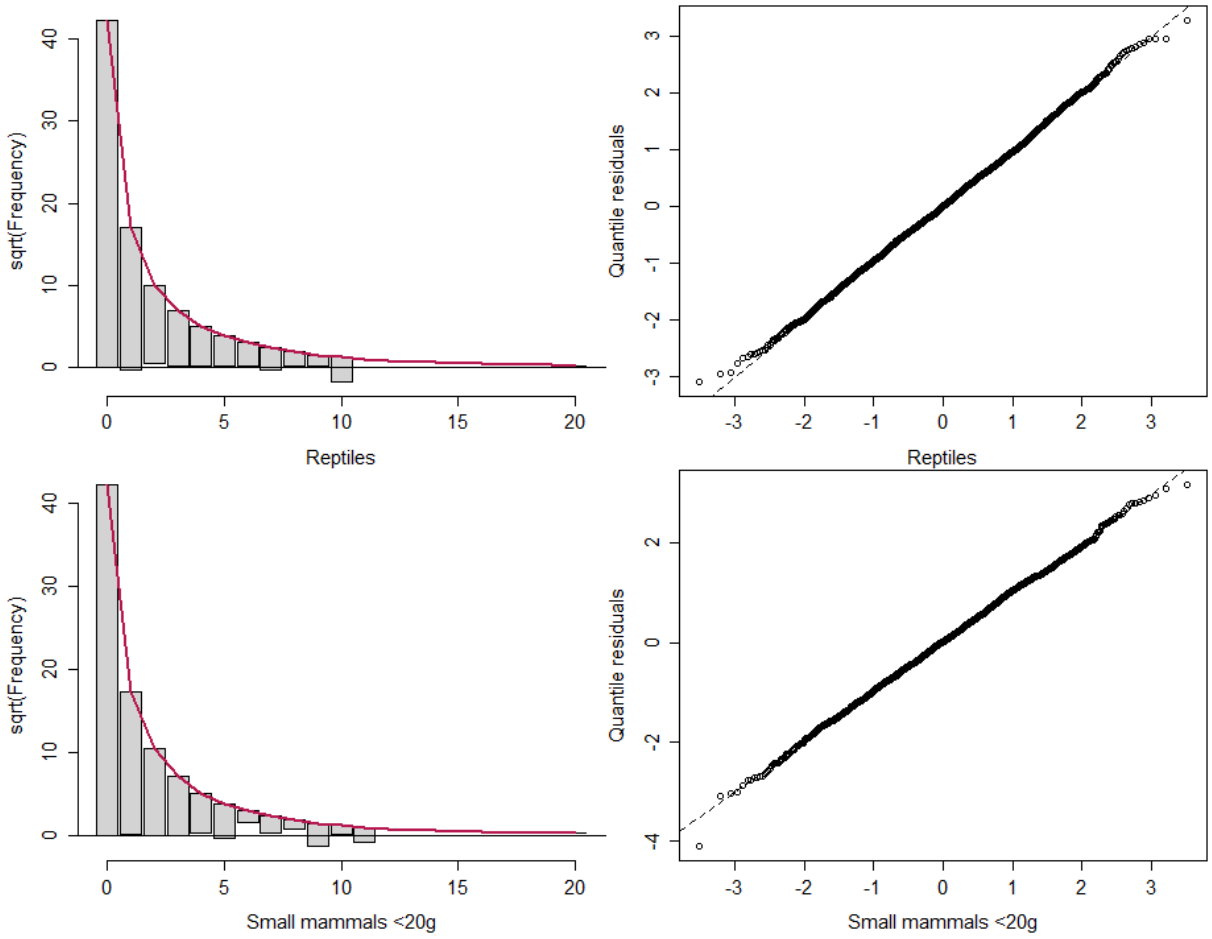
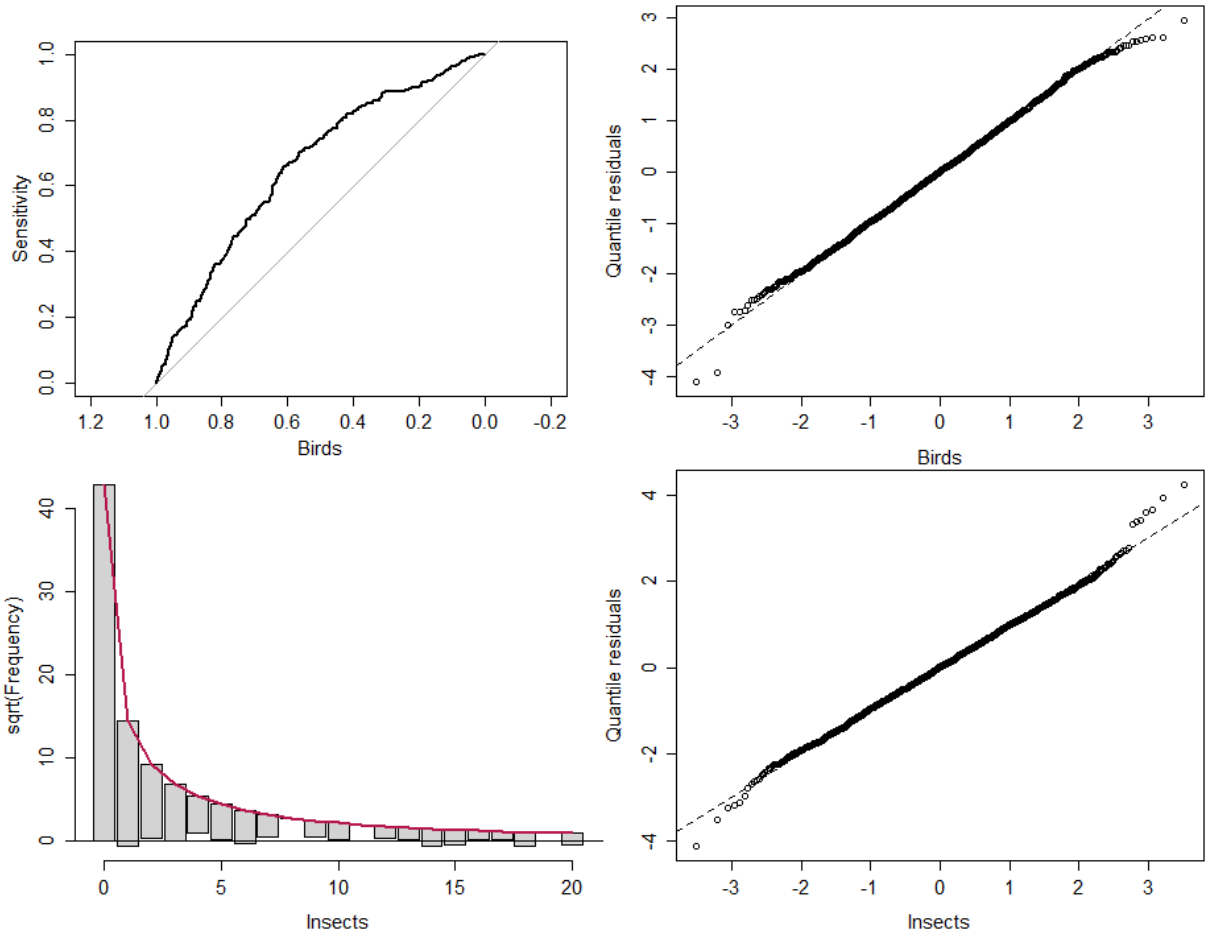

sqrt(Frequency)
Reptiles
Quantile residuals
Reptiles
sqrt(Frequency)
Small mammals <20g
Quantile residuals
Small mammals <20g

805


Sensitivity
Birds
Quantile residuals
Birds
sqrt(Frequency)
Insects
Quantile residuals
Insects

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807