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The use of point-of-view cameras (Kittycams) to quantify predation by colony cats (*Felis catus*) on wildlife

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Abstract

Context. Domestic cats (*Felis catus*) are efficient and abundant non-native predators, recently labelled as primary contributors to global biodiversity loss.

Aims. Specific research goals included determining the proportion of hunters, estimating hunting efficiency, identifying primary prey and examining predictors of kill rate and efficacy.

Methods. We investigated hunting of wildlife by stray cats living in managed outdoor colonies on a barrier island in the southeastern USA, and monitored 29 stray cats seasonally in 2014 and 2015 using Kittycam video cameras.

Key results. In total, 24 cats exhibited hunting behaviour and 18 captured prey. The estimated average daily predation rate from these successful hunters was 6.15 kills per 24-h period. Hunting effectiveness (percentage of capture attempts that translate to a kill) was an average of 44%. The most common type of prey captured was invertebrate (primarily Orthopteran and Hemipteran insects), followed by amphibians and reptiles. Eighty-three percent of kills occurred between dusk and dawn.

Conclusions. Colony location (near undeveloped island habitat) was related to higher kill rates. Cat sex and nocturnal hunting activity were related to greater hunting efficiency.

Implications. These results address the significant gap in knowledge about stray cat hunting activities, and raise conservation concerns for some groups of organisms (reptiles and amphibians) that have not been widely identified as vulnerable to cat predation.

Additional keywords: anthropogenic impacts, cat behaviour, invasive species, islands.

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Introduction

Despite their small size and somewhat docile behaviour, domestic cats (*Felis catus*) are efficient predators of many groups of wildlife, including small mammals, insects and birds (Ogan and Jurek 1997). The domestic cat is considered one of the most significant anthropogenic threats to biodiversity (Loss *et al*. 2017), particularly within island ecosystems, where they have been responsible for the extinction of at least 63 endemic vertebrates (Doherty *et al*. 2016). Free-roaming cats may also influence wildlife in other negative ways; cat presence can interfere with important natural behaviours (e.g. nesting and foraging) and cats can serve as reservoirs for pathogens significant to both public and wildlife health (Gerhold and Jessup 2013). Domestic cats are generalist predators that may exploit a wide range of prey; they are also able to readily switch prey (Fitzgerald and Turner 2000). Previous research has shown that feeding cats does not curb their natural inclination to hunt wildlife prey. For example, Barratt (1998) reported that the number of prey captured was not influenced by the number of meals provided. Davis (1957) observed that domestic cats continued to eat rats and pigeons during periods of supplemental feeding and that feeding did not decrease predation.

The fact that cats prey upon native songbirds and other wildlife is not disputed; however, the rate of wildlife take has been a major point of contention (Marra and Santella 2016). Depredation of wildlife by feral domestic cats has previously been investigated in a variety of locations across the globe, most commonly on island systems where introduced predators caused devastating effects to local wildlife, such as Hawaii, Natividad Island (Mexico), Canary Islands, Australia, New Zealand and Galapagos Islands. These studies relied on stomach content or scat analysis to document feral cat prey choice (Fitzgerald and Karl 1979; Liberg 1984; Konecny 1987; Nogales and Medina 1996; Molsher *et al*.1999; Keitt *et al*. 2002). A review of feral cat predation on islands revealed that mammals and birds were the most frequent taxa in cat diets (Bonnaud *et al*. 2011). The methodology used in the reviewed studies underestimates total predation, though, as cats do not consume every prey item. In fact, Loyd *et al*. (2013) found that pet cats ate less than a third of the prey they captured while roaming; many items were left unconsumed at the site of capture. The current range of estimates of wildlife capture per free-roaming cat varies widely, from 10.2 animals per cat per year in Australia (Barratt 1998) to 68 animals per cat per year in New York State (Kays and DeWan 2004).

An estimation of the broad impact of free-roaming cats on the wildlife of the United States suggests that up to 3.7 billion birds and 20.7 billion mammals fall prey to cats each year (Loss and Marra 2013). Stray cats are reported to be responsible for a greater proportion of the kills than pet cats, but the predation estimates included in the models for unowned cats were derived from studies reporting scat and/or stomach contents of cats. Additionally, the hunting rates used in these models may be exaggerated, because the authors utilised limited available information from two studies that included the percentage of sample cats exhibiting hunting behaviour as 100% and 90%, respectively. Furthermore, these studies reported on hunting from farm or barn cats, which are often selected by owners for hunting ability (Warner 1985). Given the significance of cat hunting behaviour to wildlife conservation, there is a need to validate current estimates and to utilise improved methodology for calculating an unowned domestic cat predation rate that more accurately represents the average impact of a free-roaming stray cat (Baker *et al*. 2008).

Predatory cat behaviour may differ by time of day and season. George (1974) analysed the behaviour of three cats and found 50% of prey captures occurred during the day, 30% at night with the remainder recorded as crespuscular. Barrat (1998) found that almost all prey returned to residences by pet cats in Australia were returned during the day. Cats may be more active during spring and summer months than during periods of extreme cold or during mid-day summer heat. George (1974) found his study cats to be more active during twilight summer hours, while Churcher and Lawton (1987) found that cats in England brought home more prey during calm, dry weather. In total, 88% of wildlife admissions to the Wildlife Center of Virginia for rehabilitation due to cat attack took place in the spring and summer (McRuer *et al*. 2017).

The amount of time spent hunting varies widely by individual, and it is well known that some cats are more active and/or successful hunters than others. Dickman and Newsome (2015) found that 55% of a sample of 113 Australian pet cats engaged in hunting wildlife and Loyd *et al*. (2013) reported that 44% of 55 suburban pet cats exhibited hunting behaviour while roaming. Whereas most owned cats spend only a portion of their day outdoors, stray cats spend 100% of their time in the environment. Even when living in managed (trap–neuter–return, or TNR) colonies, where they are sterilised and receive supplemental food, cats may spend a significant amount of time hunting or interacting with wildlife. Sterilisation does not appear to affect a cat's motivation to hunt (Spotte 2014).

Animal-borne cameras can provide a constant stream of data on the activities of free-roaming cats, allowing researchers to monitor cat activities without interfering with their natural behaviour. This technology can be useful in collecting information to fill gaps in knowledge, such as the percentage of stray cats in a group that are engaged in hunting and the predation rate of hunting colony cats. Video data can also provide information about harassment or stalking activity that may not result in a kill. We used animal-borne video cameras to study the behaviour of cats managed through a TNR program to determine the proportion of hunters, estimate their capture rate, identify primary prey and examine predictors of hunting behaviour and efficacy. We hypothesised that cat sex would not influence colony cat hunting because results from our Kittycam project on pet cats in Georgia did not indicate that age or sex were predictors. We hypothesised that habitat (developed versus undeveloped) would influence hunting, because developed locations may have more open space, a factor that was found to be a predictor of the hunting behaviour of feral cats in Australia (McGregor *et al*. 2015). Developed areas may also have more common wildlife available as prey (lizards, squirrels, etc.). We hypothesised that cats residing in colonies where there was high competition with wildlife for food may have a more urgent need to hunt for nutrition; for example, sharing the subsidised food with wildlife meant cats might not receive enough food per individual.

Materials and methods

Study area

Jekyll Island is a 2366-ha barrier island on Georgia's south-eastern coast. The 2014 USA census (U.S. Census Bureau 2014) estimates that the island has 621 permanent residents, concentrated primarily on the north side of the island. However, this number likely increases during the warmer seasons, as the island is a popular tourist destination. Much like other barrier islands, Jekyll Island is known for its well protected natural lands. The island is managed to balance both the needs of residents and visitors and to protect its natural biodiversity. The largest proportion of the island is saltmarsh; however, the terrestrial component is largely composed of evergreen maritime forest, dominated by live oaks, magnolias and pines. Much of the forest floor is dominated by saw palmetto. Tidal creeks and beachfront are also key features of Jekyll Island. The weather on Jekyll is moderate year-round, with long, hot, humid summers (May–October) and short, mild winters.

Technology

Animal-borne Crittercams (Washington, D.C.) have been implemented in many studies to provide an 'animal's-eye view' of behaviours such as hunting and intra- and interspecies interactions (most recently: American alligators, Nifong *et al*. 2013; monk seals, Wilson 2015; and bull sharks, Meynecke *et al*. 2015). Developed by National Geographic's Crittercam program, we used engineered 'Kittycams' to monitor 31 free-roaming cats living in nine managed TNR colonies. The cameras weighed ~90 g, had a water-resistant housing (7.3 cm × 4.7 cm × 2.9 cm), and attached to a cat-safe collar (Fig. 1). Kittycams were equipped with VHF transmitters so that the equipment could be found if the camera fell off of the animal. The cameras included an internal motion sensor to eliminate most of the recording while the cats were sleeping, yet be sensitive enough to pick up important activities such as stalking. The cameras had infrared lights to allow the recording of nocturnal activity. After deployment, the camera batteries lasted an average of 24 h, at which time the cameras were removed to download the videos and recharge for the next deployment.

Subjects

Although a rigorous population study has not been conducted, local managers estimate the island-wide stray cat population is ~120. Of those 120, around 50 are managed in 11 colonies by a colony cat manager. Cats managed in colonies on Jekyll Island are captured when they are identified as unowned; they are then sterilised, vaccinated against rabies and common feline pathogens, marked with an ear notch and released in the general area they were found. They do not receive additional vaccines. Cats are fed daily each morning and provided with medical care if needed.

From March 2014 to May 2014, our field technician participated in the daily feeding of these cats to habituate them to her presence. This was a crucial step to make the deployment of cameras possible because, even though cats were accustomed to the colony cat manager and his employee, they would not allow anyone else to touch them. The mere presence of a stranger often meant the cats behaved erratically and the colony managers were often unavailable to help with camera deployment. We outfitted cats with Kittycams from May to December 2014 and again from February to August 2015. Previous research noted above, as well as our own Kittycam work with pet cats, showed most hunting activity takes place during warmer seasons, such as February through November in the southeast (Loyd *et al*. 2013). Therefore, to maximise resources, we did not deploy cameras during the cooler months when prey was less abundant and cats were less active. We placed cameras on cats by quickly restraining previously habituated cats and slipping the collars over their heads. All procedures were reviewed and approved by the University of Georgia's Institutional Animal Care and Use Committee (AUP #A2010 05-091-Y3-A0).

We were able to outfit 31 cats with cameras: 12 female, 17 male and 2 unknown. The colonies were located at various forested and suburban spots on Jekyll Island (Fig. 2). Sites located in suburban neighbourhoods were categorised as 'developed', whereas those in close proximity to natural forest or beach were labelled 'undeveloped'.

Video analysis

We counted the number of hunting events (stalking, harassing and capturing) for each cat and calculated a daily kill rate for each hunting individual. We defined stalking as slow, forward locomotion directed towards prey with the cat's head kept low (Stanton *et al*. 2015). We defined harassing as any action that affected the behaviour of the prey species without killing or visibly injuring it (e.g. chasing, batting or pouncing). This also included non-lethal behaviour such as carrying prey that eventually escaped. Hunting activities, even if not resulting in capture, were critical to include because they have important sublethal effects on prey animals – for example, avian fecundity (Bonnington *et al*. 2013) – and because we could not confirm that prey did not later die of capture-related injuries. We identified captured animals to order (mostly arthropods) or species (vertebrates).

Statistical analyses

We used descriptive statistics to examine the proportion of cats exhibiting hunting behaviour and capturing prey, and to calculate a daily predation rate. We calculated an average daily

Fig. 1. Colony cat wearing research Kittycam on Jekyll Island, Georgia, USA, 2014 and Kittycam image of a captured bird in the mouth of a research subject.

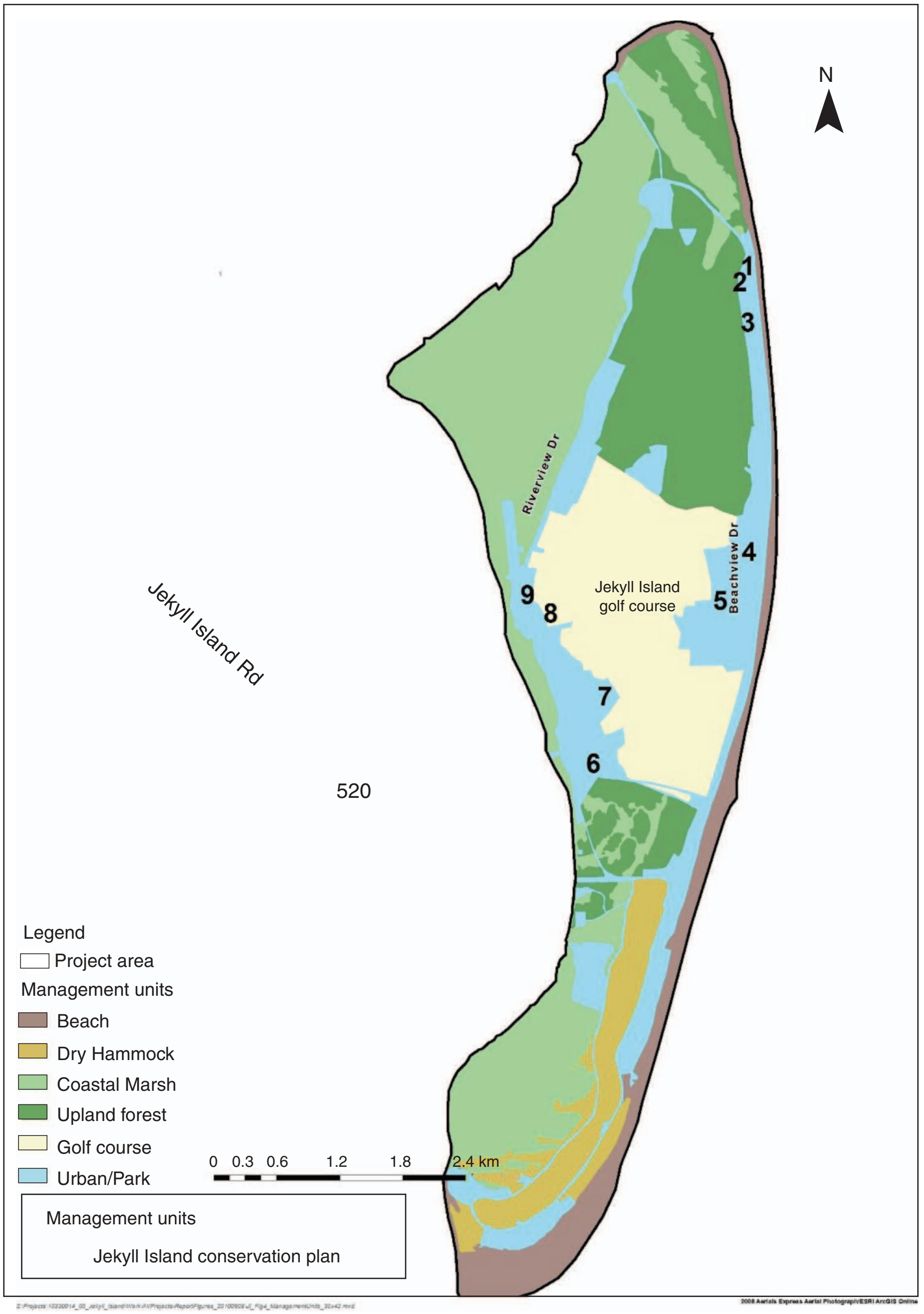

Fig. 2. Locations of cat colonies and land use on Jekyll Island, Georgia, USA. Sites located in suburban neighbourhoods were categorised as 'developed' (4, 5, 6, 7), whereas those in close proximity to natural forest or beach were labelled 'undeveloped' (1, 2, 3, 8, 9).

kill rate for each cat using the number of kills and total video hours recorded for each individual (kills per hours recorded × 24). We ran Pearson correlations to look for relationships between continuous variables and kill rate. We used General Linear Regression to investigate any possible influences on cat kill rate (using the rate rather than number of kills to help standardise data considering uneven recording times). We used the following variables as predictors: cat sex, colony location (developed or undeveloped), the number of video hours recorded, percentage of hunting activity between dusk and dawn (nocturnal activity) and competition with wildlife for food at feeding stations. This last variable was also transformed to a daily rate (average number of interactions with wildlife at feeding stations per day). The wildlife observed sharing food with cats at cat colonies primarily included raccoons and black vultures (Hernandez *et al*. 2018). We calculated hunting effectiveness for each hunter by evaluating the number of hunting attempts resulting in an animal capture. We used General Linear Regression to examine the influence of cat sex, colony location, and nocturnal activity on hunting effectiveness. We determined goodness of fit for regression models using R^2 values and by checking plots of residuals.

Results

Data from two of the 31 cats monitored were not used due to camera malfunctions during deployment. We analysed 681 h of video. We collected an average of 22 h of video (Range = 3.8–60 h) from each cat, depending on how frequently the cat could be handled. 24 of the 29 (83%) remaining sample cats exhibited hunting behaviour. 18 cats (62%) killed prey. The average daily predation rate estimated from these successful hunters was 6.15 kills per 24-h period (s.d. = 4.292, range = 0.727–17.471). Three individuals killed more than a dozen animals in one day. The average invertebrate daily predation rate was 4.95 (s.d. = 4.2, range = 0–12.6), compared with an average vertebrate daily predation rate of 4.37 (s.d. = 3.1, range = 0–16.5). The hunting effectiveness (percentage of capture attempts that translated to a kill) of an individual cat exhibiting hunting behaviour was, on average, 44% (s.d. = 34.5, range = 0–100%). For the 24 cats that were observed stalking, harassing or capturing animals, the average number of hunting activities per day was 9.84 (s.d. = 7.53, range = 1.36–28.92). The most common type of prey captured were invertebrates (primarily Orthopteran and Hemipteran insects), followed by amphibians and reptiles (Fig. 3). Hunting effectiveness varied by group, with high percentages of pursued invertebrates (82%), reptiles (69%) and amphibians (76%) captured. Hunting effectiveness was reduced for mammalian and avian prey (64% and 17%, respectively). On average, 83% of captures were consumed by the cats (88% of invertebrates, 79% of reptiles and amphibians, 78% of mammals and 50% of birds) and the remaining items were left at the site of predation. We include below a list of species killed by stray cats (for vertebrates), with invertebrates counted by order (Table 1). The average time before observing a predation event was 5.86 h of video. In total, 73% of all hunting behaviours and 83% of all kills took place between dusk and dawn. Six cats captured more than 10 animals during their monitoring period, and these were used to investigate whether hunters preferred a particular type of prey (Dickman and Newsome 2015). Of these, 71% of one cat's targets were arthropods, 65% of another's were arthropods and 56% of a third cat's were amphibians. The remaining cats' prey was more evenly divided among several groups of organisms (Fig. 3).

Regression revealed that colony location near undeveloped island habitat was the only significant predictor of the number of kills per day (kill rate) by hunting cats (β = 4.56, s.e. β = 2.12, P = 0.046, Model R^2 = 0.387) (Table 2). Cat sex, competition at colony feeding station, percentage of cat hunting activity that was nocturnal and the number of hours recorded were not found to be predictors of kill rate. However, the percentage of hunting activity between dusk and dawn was positively correlated with kill rate (Pearson correlation = 0.431, P-value = 0.031). The number of video hours recorded was strongly correlated with the overall number of kills detected (Pearson correlation = 0.916, P-value = 0.000); however, the relationship between daily kill rate and hours recorded was not significant (Pearson correlation = 0.114, P-value = 0.595). The linear regression model predicting hunting efficacy (attempts resulting in captures) had an R^2 = 0.399. The model suggested that nocturnal activity (β = 0.448, s.e. β = 0.177, P = 0.0206) and female sex (β = 0.709, s.e. β = 0.318, P = 0.038) positively influenced hunting effectiveness (Table 3; both categories of sex are presented in the results tables because one cat included in the model had unknown sex).

Discussion

Our previous research on pet cats using animal-borne cameras found that fewer individuals exhibited hunting behaviour than did the stray cats sampled in this study (44% of pet cats studied in Athens, Georgia versus 83% of stray colony cats on Jekyll Island, Georgia in this study). The primary prey captured in each location was also different, with many more amphibians and invertebrates falling prey to roaming cats on Jekyll. These results may be skewed by one particular colony cat that was recorded capturing 28 green tree frogs (*Hyla cinerea*) and seven Southern leopard frogs (*Lithobates sphenocephalus*) in 58 recording hours (66% of all amphibian prey captured). Prey type is also heavily influenced by the fact that the overwhelming majority of hunting took place at night. Invertebrates were only 21% of prey items captured by Athens' cats, who mostly roamed during the day, but invertebrates were the preferred targets on Jekyll Island. High numbers of invertebrates were also reported in the stomach contents of stray cats on other islands (Bonnaud *et al*. 2011), though, to date, there has been no other research documenting cat diet on islands off the Atlantic coast.

The average predation rate for hunting stray cats was found to be similar to a recent report from feral cats monitored with cameras in Australia (McGregor *et al*. 2015). Stray cats on Jekyll were more effective at capturing hunted prey compared with the Australian cats (44% and 30%, respectively), but this may be due to habitat differences (with no developed aspects to the property sampled in Australia) or due to the higher percentage of invertebrates targeted on Jekyll. Female cats may be more effective hunters because these skills should be selected for in the female sex, due to the increased nutrition needed to support pregnancy, lactation and care of young. This warrants further empirical research. Unlike Dickman and Newsome's (2015) results, our study cats did not seem to specialise in a particular type of prey, though this may be influenced by the small sample size (only six hunters captured more than 10 prey items). Avian prey seemed especially hard for cats to capture; 12 birds were hunted by Jekyll cats during recordings but only two were captured. It is possible that the design of the Kittycams may interfere with the specialised movements required for hunting birds (e.g. jumping upward). Although the weight of the camera was well below 3% of the cats' bodyweight (the standard for devices applied to mammals is 5%), there are no specific guidelines to standardise shape or attachment design (Millspaugh *et al*. 2012). During the

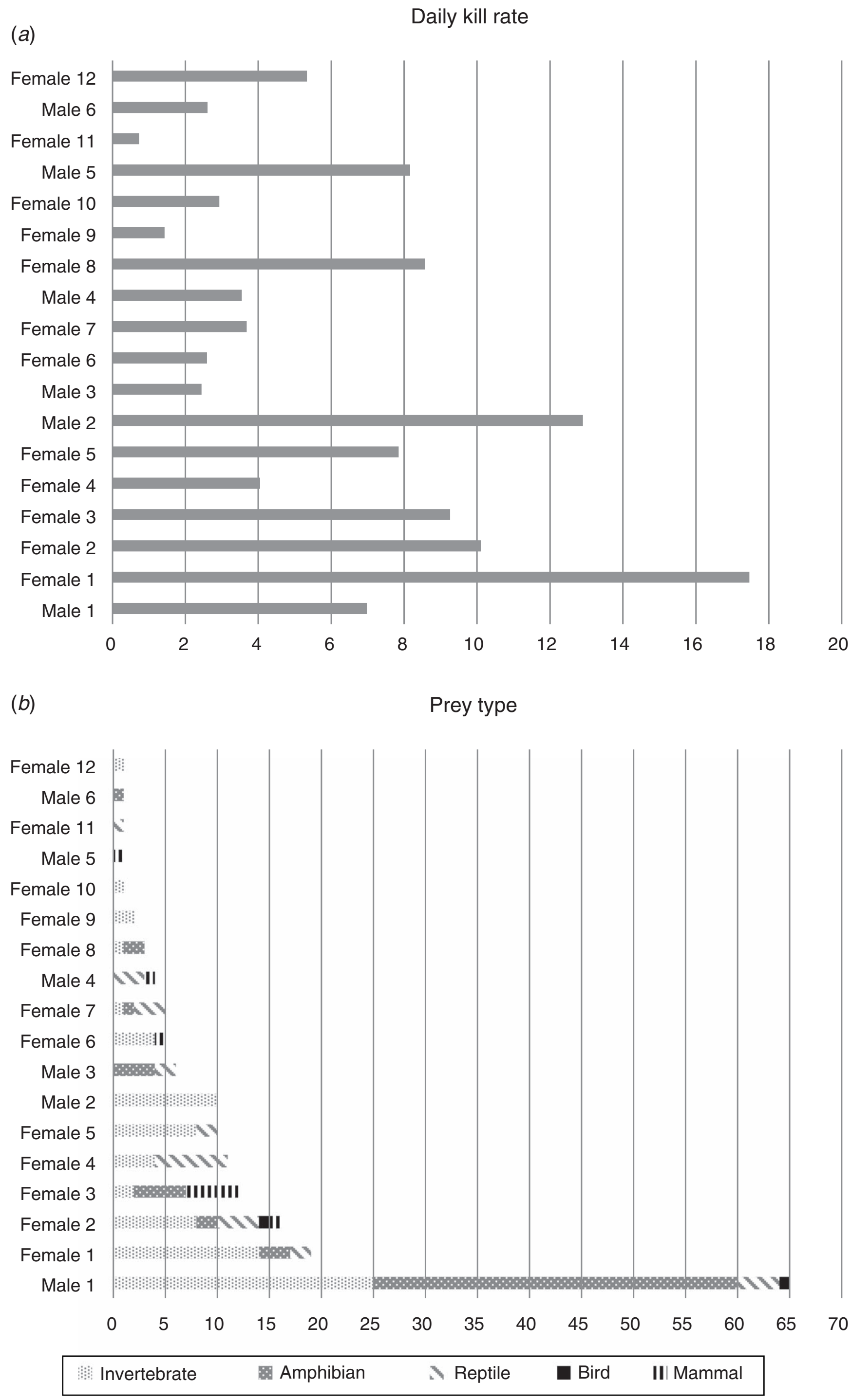

Fig. 3. Daily kill rate (*a*) and total prey captures (*b*) for 18 colony cats on Jekyll Island, Georgia, USA, 2014–15.

first 24 h after camera attachment, we carefully monitored cats for signs of intolerance to the camera – all cats moved, ate, groomed and engaged in social behaviours in a normal manner; however, subtle effects may not have been readily apparent.

The majority of the animals captured were consumed by the cats in this study (as opposed to only 28% for pet cats in the city of Athens), suggesting that although they were fed daily each morning by colony caretakers, the cats may be supplementing their diet with these kills, especially at night. With the exception of the colony located directly outside of the cat manager's home, the colony sites experienced competition for food from wildlife attracted to the feeding stations. The

Table 1. Animals killed by hunting colony cats on Jekyll Island, GA, USA (2014–15)

Species (vertebrate) or order (invertebrate)	Total number killed	Number of cats that killed
Green tree frog (*Hyla cinerea*)	29	2
Cricket, katydid, grasshopper (order Orthoptera)	29	11
Unknown insect (class Insecta)	24	8
Cicada (order Hemiptera)	20	6
Southern leopard frog (*Lithobates sphenocephalus*)	21	7
Mediterranean house gecko (*Hemidactylus turcicus*)	10	4
Green anole (*Anolis carolinensis*)	9	4
Five-lined skink (*Plestiodon fasciatus*)	8	4
Beetle (order Coleoptera)	2	2
Moth (order Lepitoptera)	2	2
Dragonfly (order Odonata)	2	1
Spider (class Arachnida)	2	1
Meadow vole (*Microtus pennsylvanicus*)	2	1
Eastern mole (*Scalopus aquaticus*)	2	1
Unknown mouse	1	1
Unknown frog or toad	2	1
Grey squirrel (*Sciurus carolinensis*)	1	1
Marsh rabbit (*Sylvilagus palustris*)	1	1
Cotton mouse (*Peromyscus gossypinus*)	1	1
Wood thrush (*Hylocichla mustelina*)	1	1
Spring peeper (*Pseudacris crucifer*)	1	1
Eastern glass lizard (*Ophisaurus ventralis*)	1	1
Broad-headed skink (*Plestiodon laticeps*)	1	1
Unknown bat (suborder Microchiroptera)	1	1
Unknown bird (order Passeriformes)	1	1

Table 2. Regression model results predicting the influence of variables on colony cat kill rate, Jekyll Island, GA, USA (2014–15)
Coef, coefficients

Term	Coef	s.e. Coef	*T*-value	*P*-value
Constant	2.46	5.10	0.48	0.636
Hours recorded	0.0299	0.0247	1.21	0.243
Competition	0.125	0.183	0.68	0.503
Nocturnal activity	2.74	2.83	0.97	0.347
Location (Undeveloped)	4.53	2.12	2.14	0.047
Sex				
F	–2.62	5.06	–0.52	0.612
M	–4.06	5.40	–0.75	0.463

Table 3. Regression model results predicting the influence of variables on colony cat hunting efficacy, Jekyll Island, GA, USA (2014–15)
Coef, coefficients

Term	Coef	s.e. Coef	*T*-value	*P*-value
Constant	–0.448	0.342	–1.31	0.205
Nocturnal activity	0.448	0.177	2.54	0.020
Location (Undeveloped)	0.027	0.127	0.21	0.834
Sex				
F	0.709	0.318	2.23	0.038
M	0.597	0.332	1.80	0.088

colony located outside the manager's home was also the only colony where food was available at all times, yet three of the four cats residing there exhibited hunting behaviour. This is consistent with Barratt (1998) and Davis (1957) regarding subsidised food failing to influence inclination to hunt. Cats are opportunistic predators and prey take is correlated with prey availability (Liberg 1984; Molsher *et al*. 1999). Green anoles (*Anolis* species), frogs of various species, house geckos (*Hemidactylus* species) and insects are widely available (seasonally) in southeastern habitats, and were captured most often by hunting cats.

Nocturnal activity as a predictor of hunting efficacy can probably be explained by the ease of capturing nocturnal prey (insects and amphibians). However, the results of the regression analyses for kill rate were surprising. Colony location did have an influence on daily kill rate, though not as predicted. We hypothesised greater hunting behaviour in developed locations but cats from colonies found close to wild, undeveloped lands made more kills. The colonies we monitored were primarily located in the northern region of the island, where the majority of the residential development is located. Sensitive shore bird species primarily nest on the southern portion of the island, where sandy beach habitat is available. The cats we monitored did not roam on beaches, where other protected species, such as loggerhead sea turtle (*Caretta caretta*) hatchlings, would be vulnerable to predation. However, we only monitored 29 of the ~50 cats managed by the colony cat manager and 24% of the total estimated number of cats on the island. Thus, it is likely that our study underestimated the impact of some domestic cats on Jekyll and missed potential impacts on sensitive species. As one example, there are outdoor cats residing on the southernmost hotel properties on the beach side of the island. These animals are provided subsidies in the form of both purposeful and incidental (garbage) feeding. The authors have personally observed these cats roaming the beach. Nonetheless, the results of this study would suggest that if TNR colonies are utilised as management tools, they should be located in habitats away from threatened wildlife species.

Conclusion

Our results contribute important details of stray cat hunting behaviour that should serve to improve future models' ability to predict free-roaming cats' broad impacts on wildlife. For example, Loss and Marra (2013) primarily considers avian and mammalian prey because so little information was available on depredation of reptiles and amphibians. Reptiles and amphibians are overlooked in estimates of cat impact on wildlife but were again found to be frequently captured by free-roaming cats. This builds on comparable Kittycam research conducted with pet cats (Loyd *et al*. 2013). Herpetofauna conservation groups have not yet joined the voices of other biologists in opposition to the maintenance of cats outdoors, but perhaps this study can help to facilitate the importance of this conservation challenge. Amphibians are experiencing declines in populations worldwide (IUCN); the primary causes are thought to be disease and pollution. Non-native predators may be an understudied and unrecognised, but significant, additive threat to herpetofauna. Population studies of prey species in similar environments with and without free-roaming cats may document population-level effects, and should be the next critical area of research on this conservation issue.

Conflicts of interest

The authors declare no conflicts of interest.

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