Title

Temporal overlaps of feral cats with prey and competitors in primary and human-altered habitats on Bohol Island, Philippines

List of Authors

Vlastimil Bogdan[1], Tomáš Jůnek[1], Pavla Jůnková Vymyslická[1]

[1]*Department of Ecology, Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Kamýcká 129, 165 21 Prague 6 – Suchdol, Czech Republic,*

Corresponding Author

Tomáš Jůnek,

Lindnerova 448/8, 180 00 Prague, Czech Republic

E-mail address: tom_junek@yahoo.com

Abstract

The vertebrate fauna of the Philippines, known for its diversity and high proportion of endemic species, comprises mainly small- to medium-sized forms with a few large exceptions. As with other tropical ecosystems, the major threats to wildlife are habitat loss, hunting and invasive species, of which the feral cat (*Felis catus*) is considered the most damaging. Our camera-trapping study focused on a terrestrial vertebrate species inventory on Bohol Island and tempo-spatial co-occurrences of feral cats with their prey and competitors. The survey took place in the Rajah Sikatuna Protected Landscape, and we examined primary rainforest, its border with agricultural land, and rural areas in the vicinity of villages. Altogether, ~~in~~ over 2,885 trap days we captured 30 species of vertebrates – 10 mammals (including *Sus philippensis*), 19 birds and one reptile, *Varanus cumingi*. We trapped 81.8% of expected vertebrates. Based on the number of independent events, the most frequent native species was the barred rail (*Gallirallus torquatus*). The highest overlap in diel activity between cats and potential prey was recorded with rodents in rural areas (Δ=0.62); the lowest was in the same habitat with ground-dwelling birds (Δ=0.40). Cats were not recorded inside the rainforest; in other habitats their diel activity pattern differed. The cats' activity declined in daylight in the proximity of humans, while it peaked at the transition zone between rainforest and fields. Both rodents and ground-dwelling birds exhibited a shift in activity levels between sites where cats were present or absent. Rodents tend to become active by day in cat-free habitats. No temporal response to co-occurrences of civets (*Paradoxurus hermaphroditus* and *Viverra tangalunga*) was found. Our first insight into the ecology of this invasive predator in the Philippines revealed an avoidance of homogeneous primary rainforest and a tendency to forage close to human settlements in heterogeneous habitats. A detailed further investigation of the composition of the cat's diet, as well as ranging pattern, is still needed.

Commented [v1]: Indicate over what time period.

Introduction

The Philippine Archipelago is considered a global biodiversity hotspot, known for its high proportion of endemic species (Ambal *et al.* 2012). The terrestrial vertebrate taxa, which primarily encompass~~es~~ small to medium sized species, inhabit more than 7100 islands. These species include at least 213 mammals (Heaney *et al.* 2010), 674 birds (Lapage 2015), 270 reptiles and 111 amphibians (BREO 2015).

Similar~~ly~~ to other oceanic islands, the predominantly small fauna of the Philippines suffer~~s~~ from the presence of competing invasive species, such as *Rattus* spp., and the feral cat (*Felis catus*). The cat is listed as the most widespread and probably most damaging of the four carnivores included on the list of the 100 worst invasive species (Lowe *et al.* 2000). At least 175 vertebrates are threatened or have been driven to extinction by feral cats on at least 120 islands (Medina *et al.* 2011). Meta-analysis has revealed that the negative impact of feral cats is largest for insular endemic mammals, and is exacerbated by the presence of invasive cat prey species such as mice or rabbits (Nogales *et al.* 2013). The cat is widely kept as a pet by people throughout the Philippines and can be found foraging in every habitat (Duffy & Capece 2012). Despite the general prevalence of cats in the Philippine landscape, there is a noticeable lack of knowledge regarding the cat's impact on the biodiversity of this archipelago.

Commented [v2]: Provide Latin names.

Cats feed on a wide range of animals, from arthropods, reptiles and birds to mammals the size of a rabbit (Pearre, Maass & Maass 1998). In Australia alone, with a variety of animals of similar size such as those found in the Philippines, ~~has recorded~~ 400 prey species consumed by cats have been recorded (Doherty *et al.* 2015). In the Philippines, members of the orders Chiroptera and Rodentia are the most numerous mammalian species (Heaney *et al.* 2010). A wide range of terrestrial and arboreal rodents with body mass ranging from the 15-g *Musseromys* spp. to the 2.6-kg *Phloeomys* spp. risk predation by cats. Only adult individuals

of *Phloeomys* and *Hystrix pumila* (Heaney *et al.* 2010) exceed the potential prey dimensions. According to size and niche, members of the Tupaiidea (treeshrews), Erinaceidae (moonrats) and Soricidae family (shrews) should be listed as mammalian prey for cats. Similarly, the smallest Philippine primate, *Tarsius syrichta*, which inhabits Bohol and other islands of the Mindanao faunal region, can be included (MacKinnon & MacKinnon 1980).

On Bohol Island (3,269 km^2), as on the other Philippine islands, bats and rodents dominate among local mammals. The ~~s~~Small mammalian fauna consists of one insectivorous species and nine species of rodents, including the introduced *Mus musculus*, *Rattus rattus*, *Rattus norvegicus*, *Rattus tanezumi* and *Rattus exulans* (Heaney *et al.* 2010). The avifauna of Bohol numbers 235 species, with Passeriformes forming the largest sub-group at 83 species. Bohol is also home to 14 ground-dwelling bird species inhabiting the woody or bushy inland habitats potentially affected by cats (Kennedy 2000).

Along with dog (*Canis lupus familiaris*), possible competitors of cats on Bohol include two mammalian carnivores, Asian palm civet (*Paradoxurus hermaphroditus*) and Malayan civet (*Viverra tangalunga*) (Heaney *et al.* 2010) and two reptile species~~:~~, Cuming's water monitor (*Varanus cumingi*) and reticulated python (*Python reticulatus*) (BREO 2015).

Tempo~~-~~spatial co-occurrence of competing species from camera trapping data was examined for example in the Sumatra forest on felids from the size of the marbled cat to the tiger (Sunarto *et al.* 2015) and in Australia between dingoes and the feral cat (Wang & Fisher 2012). Results based on the overlapping diel activities confirmed the potential in description of the timing of the activity in response both to the presence of superordinate predators and also in temporal partitioning between the same-sized predators or predators of the same-sized prey. The f~~F~~eral cat as an invasive mesopredator which could be suppressed by the presence of apex predators ~~could be~~ within invaded habitats~~, suppressed by apex predators which has~~ a

Commented [v3]: You need a sentence at the beginning of this paragraph, outlining what overlaps in activity tell us about likely interactions.

Commented [v4]: Provide Latin name

Commented [v5]: Provide Latin name

Commented [v6]: Currently this sentence doesn't make sense, to the extent that I can't re-write it.

with direct implications for wildlife management, especially ~~mainly~~ when the dominant one is limited (Brook, Johnson & Ritchie 2012).

Commented [v7]: It is not clear what you mean here.

We conducted a camera-trap survey on Bohol Island in an attempt to uncover tempo-spatial co-occurrences of terrestrial vertebrate species on regularly used trails with the confirmed presence of cats in the protected primary rainforest (Zone I), a transition zone along the border of the primary rainforest with the agricultural landscape (Zone II), and inside the rural landscape in the proximity of human settlements (Zone III). Our objectives were to: (1) ~~Create~~ create a general inventory of camera-trapped taxa; ~~,~~ (2) ~~Model~~ model the species accumulation curve using previous knowledge of the possible number of mammalian, avian and reptile species detectable by camera-traps; ~~,~~ and (3) ~~Compare~~ compare the diel activity levels of cats with those of potential prey and competitors.

Materials & Methods

Study site

Our study was conducted under research permit No. 2014-04, issued by DENR, Region VII, Philippines, between July 2nd and December 4th, 2014 in the surroundings of the town of Bilar, Bohol Island, Philippines. The landscape consists of a mixture of distinctive flat rural areas near human settlements, used as rice fields and plantations for various crops, steep karst hills covered by brush and secondary forest, and primary rainforest in protected areas. The town of Bilar lies between two conservation areas, the Rajah Sikatuna Protected Landscape (RSPL) and the Loboc River Watershed Forest Reserve. RSPL is the second largest protected sanctuary on Bohol, covering 11,034 ha of a mostly hilly limestone environment rich in characteristic landforms such as ravines, sinkholes and caves. The altitude in RSPL varies between 300 and 826 m above sea level. The forest canopy is multi-layered, with trees reaching up to 20 m in height. Members of the families Dipterocarpaceae, Moraceae and Melicacea dominate the canopy. Certain regions of RSPL have been reforested

with white teak (*Gmelina arborea*) and Honduras mahogany (*Swietenia macrophylla*) (Barcelona *et al.* 2006). The average annual precipitation reaches 1,600 mm; the rainy season typically lasts from June to December, with an increase in precipitation to 200 mm per month. The driest month is April when approximately 40 mm of rain falls.

Sampling design

We monitored three types of landscape typical of tropical regions and deployed cameras in groups, one camera per location, at eight trapping sites (Fig. 1): Zone I – protected primary rainforest including the Watershed Forest Reserve (site WS), interior of RSPL (site SP) and abandoned farms in the early stages of succession into RSPL (site SF); Zone II – transition zone between the primary rainforest of RSPL and rice fields close to the village of Bulak (site BU), transition zone between RSPL and rice and corn fields close to Logarita Springs (site LS), and transition zone between RSPL and the farms of the village Binantay (site BI); Zone III – mixture of brush and degraded forest and plantations on the edge of the village of Subayon (site SU), and at Bohol Habitat Conservation Center on the edge of the town of Bilar (site HB).

Sampling procedures

We used 41 weatherproof infrared digital camera traps – 29 units of Ltl Acorn 5210MC (Shenzhen Ltl Acorn Electronics Co., Ltd.) and 12 units of SPYPOINT IR7 (SPYPOINT^{MD}, G.G. Telecom). Prior to the study, we tested both types of cameras in a week-long trial which was focused on the difference in detection rates for moving objects. No difference larger than 10 % between numbers of independence events was found. Both types of cameras were also used in every habitat to avoid a bias from site-specific detection rates. Cameras were set up to perform the same delay between recordings – SPYPOINT to take ~~2~~ two images with a delay of 10 s~~ec.~~ between consecutive triggering, and Ltl Acorns to take one

picture followed by a 5 s ~~sec.~~ video, with a 5 s ~~sec.~~ delay between triggering. Video sequences served as an additional tool for the identification of species.

We placed all cameras opportunistically on the most frequented trails or their junctions and, according to the expected size of target vertebrates, we fastened cameras with a belt onto the trunks of trees or bushes nearest to the trail, at a height of up to 0.5 m, with a focal point approximately 2 m~~eters~~ from the lens. All cameras were active 24 hours a day; all records in infrared mode were available only in a black-and-white version. No bait was used.

Identification of taxa

Two observers, VB and TJ, independently identified all species visually from images and videos; the results were mutually crosschecked, and disagreeing or unidentifiable records were excluded from the analysis. Based on available databases (Heaney *et al.* 2010; BREO 2015; Lapage 2015), we made a list of terrestrial mammalian and avian ground-dwelling species known or expected to occur on Bohol (Table 2). From reptiles, we included only the largest four-legged taxon, the yellow-headed water monitor (*Varanus cumingi*). Members of the order Chiroptera and the strictly arboreal Philippine colugo (*Cynocephalus volans*) were *a priori* omitted. The conservation status of each species was assessed following IUCN (2015).

Due to the limited nature of the recordings, for the identification process and the calculation of a species accumulation curve all taxa the size of a mouse (*Mus musculus* and also the insectivorous *Crocidura beatus*) were pooled into the group called 'mice', and all species of rats (*Rattus* spp. and *Bullimus bagobus*) into the group 'rats'. In addition, both known species of squirrels (*Exilisciurus concinnus* and *Sundasciurus philippinensis*) were grouped into one taxon: 'squirrels'. For purposes of *overlap* analyses between cats and their competitors and prey, we pooled both native carnivore species into a group called 'civets' and put mice, rats and squirrels into the group 'rodents'. Ground-dwelling species of birds were the second analyzed group of prey.

Data analysis

Photographs were defined as independent events (or activity records) when the delay between two consecutive images of an individual exceeded 10 min. For each species and Zone, in Table ~~1~~ 2 we reported occurrences of species at cameras represented by independent events (Lazenby & Dickman 2013).

We used a species accumulation curve based on the cumulative number of camera-trapping days, computed in EstimateS Version 9.1.0 (Colwell 2013), to find out if our survey lasted a sufficient number of days to capture the 22 selected terrestrial vertebrate species known from Bohol. We followed Tobler *et al.* (2008) and calculated well-performing estimators of species richness: the non-parametric abundance-based estimator ACE, and the non-parametric incidence-based estimators ICE and Jackknife 1. An abundance-based rarefaction approach with 95% confidence intervals and 1,000 random iterations of sample order was used.

The pair-wise temporal overlap of selected activity patterns was analyzed using the R statistical environment package '*overlap*' (Meredith & Ridout 2014). Following Ridout and Linkie (2009), we applied kernel density estimation on circular data pooled within all study sites. The coefficients of overlap (Δ) were calculated with a smoothing parameter of 1.0. We used a smoothed bootstrap of 10,000 resamples to determine standard errors and 95% confidence intervals. We only analyzed combinations of pairs of species, which scored at least 30 independent events in the activity record (Ridout, pers. comm.) in a given environment. The n~~N~~umber of independent events used for calculation of the activity pattern overlap for each analyzed group of animals and each location is shown in Table 3.

Results

Species inventory

Commented [v8]: But these could be the same individual at different times? Are they truly independent then?

Commented [v9]: But in the previous section you said you combined species into taxa to estimate the spp accumulation curve. So it is not clear how it was used to reveal whether you had captured all 22 species.

During the whole survey period, lasting 155 days, we ~~managed to~~ accumulated 2,885 trap days and 2,034 independent events. The combined capture rate across all sites was 73.1 events per 100 trap days. The list of all 30 animal taxa recorded is shown in Table 2. The most frequent native species was the barred rail (*Gallirallus torquatus*), captured in 183 independence events. We did not record four expected bird species: *Megapodius cumingii*, *Coturnix chinensis*, *Turnix sylvaticus* and *Gallinago megala*. On the other hand, we ~~succeeded in~~ confirmed~~ing~~ the survival of the Philippine warty pig (*Sus philippensis*). Given its size, it was probably a male individual that was captured, only once, on three images on August 9th (6:35 pm) in a mud wallow in the interior of RSPL (Fig. 2).

We found that feral cats most often occurred in ~~the~~ Zones II and III, and ~~we did not record any cats~~were absent inside the primary forest. A similar trend was found for ground-dwelling birds. Most rats and other small mammals were recorded in the transition Zone II between the RSPL forest and agricultural land. Along with feral cats and domestic dogs, we also recorded all three medium-sized mammals occurring on Bohol – the common palm civet (59 events), Malay civet (16 events) and long-tailed macaque (*Macaca fascicularis*) (7 events). Humans were also captured but excluded from the analysis.

Within all eight sampling sites, we captured 18 of 22 previously specified target taxa, which corresponds to a success rate of 81.8% ~~in~~ of the species inventory (100% of mammals and reptiles, 69.2% of birds). We used these 18 taxa for calculating the species accumulation curve (Fig. 3). The mean estimated species richness computed in EstimateS was 19.~~6~~7 species (ACE = 19.6~~55~~, ICE = 19.5~~47~~ and Jackknife 1 = 20.0~~19.99~~). We recorded 15.89 species (72.2% of expected species) in 1,000 trap days. The eight target species of mammals were captured in 1,723 trap days; similarly, nine ground-dwelling birds were recorded within 1,435 trap days.

Temporal overlaps

Commented [v10]: You should remove this figure. Adjust the numbering of the others accordingly.

We recorded cats only in transition Zone II and inside the rural landscape in the proximity of close to human settlements (Zone III). Diel activity patterns of cats differed among zones (Figure 4). Cats showed a decrease in the late late afternoon activity near villages, whereas activity in the transition area peaked right before noon. Generally, the activity of cats by daylight was higher in transition zones; in secondary urban areas cats were recorded mainly at night.

The highest overlap in the activity patterns between cats and rodents (Table 4) was found in the rural landscape of Zone III, and between cats and ground-dwelling birds in transition Zone III (Fig. ure 5).

Both categories of potential prey showed shifts in temporal occurrence within sites, based on the presence of cat (Fig. ure 6). As seen, the peaks of rodent activity decreased in the hours before sunrise and increased after sunset, whereas the activity of ground-dwelling birds peaked about 4 hours sooner at sites where cats were not recorded.

The overlap between the diel activity patterns of cats and both species of civets is shown in Figure 7. Cats exhibited roughly consistent activity throughout a 24-hour period, with no apparent shift caused by the nocturnal occurrence of sympatric civets.

Discussion

According to our knowledge, to date, no study of the behavior and ecology of feral cats has been conducted in the Philippines, nor any camera-trap-based species inventory on Bohol. With the exception of the Philippine pygmy squirrel, *Exilisciurus concinnus*, we were able to capture and identify every non-volant mammalian species recorded as occurring on Bohol larger than a mouse, including an individual of *Sus philippensis*, which is considered to be close to extinction (Oliver 1993), even by local people. Compared to known species, eCamera traps captured 81.8% of known ground-dwelling mammalian, avian, and reptilian

Commented [v11]: What are these?

248 species, similar to the 86 % captured in the Amazon ~~moist~~ rain forest (Tobler *et al.* 2008) or
249 89% in the lowland rainforest of Borneo (~~89%,~~ Bernard *et al.* 2013); both those camera-
250 trapping studies were restricted to mammals. In addition, the initially steep shape of our
251 general species accumulation curve corresponds with ~~these~~ studies conducted in tropical
252 ecosystems and confirms the robustness of the approach. Similarly to Rovero *et al.* (2014), we
253 captured the majority of selected species in 1,000 trap days, considered a reliable threshold
254 enabling the detection of rare species (O'Brien 2011).
255 The absence of cats in the interior of primary rainforest seems not to be driven by
256 distance from the nearest human settlements, given that all three monitored sites were up to
257 approximately~~.~~ 3 km from houses. We suggest that ~~this could result from~~ the absence of
258 preferred features and habitats in the rain forest may have resulted in camera traps failing to
259 capture cats. ~~cats preferred habitat.~~ Cats typically use a mixture of vegetation cover at ~~a level~~
260 ~~of~~ ground level which provides both cover and open space for observing their prey; ~~and~~ such
261 habitat may increase hunting success (Doherty, Bengsen & Davis 2015). The habitat
262 heterogeneity hypothesis by Tews *et al.* (2004) predicts that heterogeneous habitats offer a
263 greater diversity and density of potential prey than homogeneous ones, which could be
264 conceivable for cats. Linear features in space (e.g. tree lines, roads and other corridors) are
265 generally considered to maximize cat's detectability (Crooks 2002; Bengsen, Butler &
266 Masters 2012). Cats, knows as users of trails (Trolle & Kéry 2005; Harmsen *et al.* 2010; Anile
267 *et al.* 2014), in the Zone I theoretically could disperse in the undergrowth in homogeneous
268 forest without linear landscape features, so camera traps on trails might be avoided.
269 The presence of competing predators in primary forest ~~also can hardly~~is unlikely to
270 explain the absence of cats. ~~cats' absence.~~ Almost all dogs recorded throughout the surveyed
271 sites were accompanying humans who passed by the cameras. Both species of civets were
272 equally present in all three zones with a distinctive nocturnal activity pattern. The common

Commented [v12]: This section isn't logical as written. First you state that cats use trails, and then you go on to say they might avoid the trails the cameras are place on in the rainforest. Could you resolve this.

palm civet and Malay civet are ~~partly~~ omnivorous (Jennings *et al.* 2009) but they forage ~~at~~ in the habitat of cats, and given their ~~and according to their~~ size we ~~can~~ consider them to be competitors ~~for~~ of cats. ~~Despite this premise~~Nonetheless, cats do not show any temporal avoidance, ~~which refers to their~~indicating a neutral co-occurrence evolved during almost a 500-year co-existence (Jubair 1999). For a more comprehensive view of possible niche partitioning, as found for example between felids on Sumatra (Sunarto *et al.* 2015), a camera-trapping study should be conducted on Negros, where the Visayan leopard cat (*Prionailurus bengalensis* ssp. *rabori*) occurs as ~~the~~ a regional direct competitor (IUCN 2015).

Our results (Table 3) show that the availability of both prey categories ~~,(~~ rodents and birds~~),~~ was higher, nearly by orders of magnitude, in both human-altered zones than in primary rainforest. We ~~link this finding with a~~attribute this to the variety of vertebrate and invertebrate prey, which is more abundant in ~~a~~ heterogeneous landscapes. In addition, as suggested by Lozano *et al.* (2003), feral cats use a wide range of habitat components to meet their different activity requirements (e.g. hunting, resting), and this landscape offers ~~such~~ a mixture of agricultural ~~landscape~~ features with secondary growth and infrastructure. The other reason for the absence of cats in primary forests could be the fact that cats are kept as pets around the world, and even feral cats benefit from human subsidies and leftovers (Ferreira *et al.* 2011). Our data clearly support such a tendency to forage relatively close~~r~~ to human settlements~~, even if~~, however we were not able to determine from our records whether a photographed animal was feral or domestic.

Although the ~~general recorded~~ diel activity pattern of cats was roughly consistent over ~~showed a roughly~~ 24 -h~~our consistency~~ periods (Fig~~ure~~ 7), a detailed analysis of zones ~~uncovered~~ revealed a decline in ~~the~~ diurnal activity ~~rate~~ in the vicinity of villages, in contrast ~~with~~ to an apparent activity peak before noon in Zone II (Figure 4). Both Zones II and III offered ~~roughly~~ more-or-less the same number of prey species (Table 2). We could

Commented [v13]: The logic behind this reason isn't clear. Cats are known to exist independently of human subsidies.

hypothesize that subsidies provided by humans in villages during the day resulted in cats remaining inactive in shelters and foraging at night. Another possible ~~cause~~ reason could be the ~~registered~~ tendency ~~of~~ for rodents to be active even during daylight (Fig~~ure~~ 5) in the transition zone, ~~and this can~~which could attract cats. Other prey ~~, which was~~ not recorded by cameras~~,~~ might also be present (e.g. large insects, lizards). ~~As shown (Figure 6), p~~Prey species ~~performed certain~~showed shifts in diel activity patterns between sites where cats were, or were not, present (Fig. 6). When cats were absent, rodents tended to forage visibly by day, while the activity of ground-dwelling birds peaked about 4 hours later. ~~We cannot clarify~~It is difficult to interpret the shift in bird activity~~s~~; one ~~hypothetical~~ reason could be a disproportion in the number of records from sites with and without cats. Rodents shift their activities to become nocturnal if cats are present and more diurnal (Doherty *et al.* 2015). This raises the question ~~is if~~ of whether almost 500 years of cat presence in the Philippines has driven adaptive mechanisms of prey and competitors to cope with a new predator or not. Our results ~~may~~ suggest that this already happened, similarly to the 4000-year history of the dingo in Australia (Carthey & Banks 2012). Nevertheless, we believe that further research is needed, especially throughout all ~~annual~~ seasons.

Knowledge of feral cat diet is paradoxically the least ~~known~~ researched in tropical habitats with the richest terrestrial biodiversity (Doherty *et al.* 2015; Doherty, Bengsen & Davis 2015). Our findings ~~uncover the first~~reveal tempo-spatial co-occurrences between feral cats and their potential prey in a typical mixture of Philippine landscapes. We confirm~~ed~~ that camera traps are capable of capturing small bodied fauna, ground-dwelling birds and highly elusive species, such as *Sus philippensis*, as well. Endangered Philippine fauna exposed to invasive species should rapidly become the target of a broad and long-term camera-trapping inventory survey. For an in-depth ~~deep~~ knowledge of the dietary intake of feral cats in the Philippines, DNA analysis of scat is ~~recommendable, and this should be~~

Commented [v14]: It is not clear what is meant here.

~~prioritized~~recommended as a priority for ~~by~~ researchers (Nogales *et al.* 2013). In addition, collared and GPS-tracked cats would provide ~~definite~~ information about habitat use and the size of home ranges. Finally, attention should be paid to the cultural value of cats kept as pets within Philippine society~~, since the beginning of the era of European colonization, mainly in terms of the~~to inform eradication strategies. ~~efficiency of eradication efforts.~~

Acknowledgements

We would like to acknowledge the following persons and organizations which made our study possible: Mr. Isabelo R. Montejo, regional director, and Mr. Eusalem S. Quiwag from the Department of Environment and Natural Resources (DENR), Region VII, Philippines; the staff of Rajah Sikatuna PL; Ms. Cristy Burlace and staff from Habitat Bohol; Dr. Petr Anděl from the Czech University of Life Sciences Prague; and Ms. Monika Drimlová for field work.

References

Ambal, R.G.R., Duya, M. V, Cruz, M.A., Coroza, O.G., Vergara, S.G., Silva, N. De & Molinyawe, N. (2012) Key Biodiversity Areas in the Philippines : Priorities for Conservation. *Journal of Threatened Taxa*, **4**, 2788–2796.

Anile, S., Ragni, B., Randi, E., Mattucci, F. & Rovero, F. (2014) Wildcat population density on the Etna volcano, Italy: A comparison of density estimation methods. *Journal of Zoology*, **293**, 252–261.

Barcelona, J.F., Dolotina, N.E., Madroñero, G.S., Granert, W.G. & Sopot, D.D. (2006) The ferns and fern allies of the karst forests of Bohol Island, Philippines. *American Fern Journal*, 1–20.

Bengsen, A.J., Butler, J.A. & Masters, P. (2012) Applying home-range and landscape-use data to design effective feral-cat control programs. *Wildlife Research*, **39**, 258–265.

347 Bernard, H., Ahmad, A.H., Brodie, J., Giordano, A.J., International, L. & York, N. (2013)
348 Camera-Trapping survey of mammals in and around Imbak Canyon Conservation Area
349 in Sabah Malaysian Borneo. *The Raffles Bulletin of Zoology*, **61**, 861–870.
350 BREO. (2015) Biodiversity Research and Education Outreach—Philippines,
351 Http://philbreo.lifedesks.org/
352 Brook, L.A., Johnson, C.N. & Ritchie, E.G. (2012) Effects of predator control on behaviour
353 of an apex predator and indirect consequences for mesopredator suppression. *Journal of*
354 *applied ecology*, **49**, 1278–1286.
355 Carthey, A.J.R. & Banks, P.B. (2012) When does an alien become a native species? A
356 vulnerable native mammal recognizes and responds to its long-term alien predator. *PLoS*
357 *One*, **7**, e31804.
358 Colwell, R.K. (2013) EstimateS: Statistical estimation of species richness and shared species
359 from samples. Version 9.1.0. User's Guide and application.
360 Crooks, K.R. (2002) Relative sensitivities of mammalian carnivores to habitat fragmentation.
361 *Conservation Biology*, **16**, 488–502.
362 Doherty, T.S., Bengsen, A.J. & Davis, R.A. (2015) A critical review of habitat use by feral
363 cats and key directions for future research and management. *Wildlife Research*, **41**, 435–
364 446.
365 Doherty, T.S., Davis, R.A., Etten, E.J.B., Algar, D., Collier, N., Dickman, C.R., Edwards, G.,
366 Masters, P., Palmer, R. & Robinson, S. (2015) A continental- scale analysis of feral cat
367 diet in Australia. *Journal of Biogeography*, **42**, 964–975.
368 Duffy, D.C. & Capece, P. (2012) Biology and Impacts of Pacific Island Invasive Species. 7.
369 The Domestic Cat (Felis catus) 1. *Pacific Science*, **66**, 173–212.
370 Ferreira, J.P., Leitão, I., Santos-Reis, M. & Revilla, E. (2011) Human-related factors regulate

371 the spatial ecology of domestic cats in sensitive areas for conservation. *PLoS ONE*, **6**, 1–
372 10.

373 Harmsen, B.J., Foster, R.J., Silver, S., Ostro, L. & Doncaster, C.P. (2010) Differential use of
374 trails by forest mammals and the implications for camera-trap studies: A case study from
375 Belize. *Biotropica*, **42**, 126–133.

376 Heaney, L.R., Dolar, M.L., Balete, D.S., Esselstyn, J.A., Rickart, E.A. & Sedlock, J.L. (2010)
377 Synopsis of Philippine Mammals, Http://archive.fieldmuseum.org/philippine_mammals/

378 IUCN. (2015) The IUCN Red List of Threatened Species. Version 2015.1.,
379 http://www.iucnredlist.org

380 Jennings, A.P., Veron, G., Wilson, D.E. & Mittermeier, R.A. (2009) Family Viverridae
381 (civets, genets and oyans). *Handbook of the mammals of the world*, **1**, 174–232.

382 Jubair, S. (1999) *Bangsamoro, A Nation under Endless Tyranny*. IQ Marin.

383 Kennedy, R. (2000) *A Guide to the Birds of the Philippines*. Oxford University Press.

384 Lapage, D. (2015) Avibase – The Word Bird Database, Http://avibase.bsc-eoc.org/

385 Lazenby, B.T. & Dickman, C.R. (2013) Patterns of Detection and Capture Are Associated
386 with Cohabiting Predators and Prey. *PLoS ONE*, **8**.

387 Lowe, S., Browne, M., Boudjelas, S. & De Poorter, M. (2000) *100 of the World's Worst*
388 *Invasive Alien Species: A Selection from the Global Invasive Species Database*. Invasive
389 Species Specialist Group Auckland,, New Zealand.

390 Lozano, J., Virgós, E., Malo, A.F., Huertas, D.L. & Casanovas, J.G. (2003) Importance of
391 scrub–pastureland mosaics for wild-living cats occurrence in a Mediterranean area:
392 implications for the conservation of the wildcat (Felis silvestris). *Biodiversity &*
393 *Conservation*, **12**, 921–935.

MacKinnon, J. & MacKinnon, K. (1980) The behavior of wild spectral tarsiers. *International Journal of Primatology*, **1**, 361–379.

Medina, F.M., Bonnaud, E., Vidal, E., Tershy, B.R., Zavaleta, E.S., Josh Donlan, C., Keitt, B.S., Corre, M., Horwath, S. V & Nogales, M. (2011) A global review of the impacts of invasive cats on island endangered vertebrates. *Global Change Biology*, **17**, n/a–n/a.

Meredith, M. & Ridout, M.S. (2014) overlap: estimates of coefficients of overlapping for animal activity patterns. R package version 0.2. 2.

Nogales, M., Vidal, E., Medina, F.M., Bonnaud, E., Tershy, B.R. & Campbell, K.J. (2013) Feral Cats and Biodiversity Conservation: The Urgent Prioritization of Island Management. *BioScience*, **63**, 804–810.

O'Brien, T.G. (2011) Abundance, density and relative abundance: a conceptual framework. *Camera Traps in Animal Ecology* pp. 71–96. Springer.

Oliver, W.L.R. (1993) Pigs, Peccaries, and Hippos Status Survey and Conservation Action Plan. *IUCN, Gland*, p.219.

Pearre, S., Maass, R. & Maass, R. (1998) Trends in the prey size-based trophic niches of feral and House Cats Felis catus L. *Mammal Review*, **28**, 125–139.

Ridout, M.S. & Linkie, M. (2009) Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, **14**, 322–337.

Rovero, F., Martin, E., Rosa, M., Ahumada, J.A. & Spitale, D. (2014) Estimating Species Richness and Modelling Habitat Preferences of Tropical Forest Mammals from Camera Trap Data (ed D Russo). *PLoS ONE*, **9**, e103300.

Sunarto, S., Kelly, M.J., Parakkasi, K. & Hutajulu, M.B. (2015) Cat coexistence in central Sumatra: ecological characteristics, spatial and temporal overlap, and implications for management. *Journal of Zoology*, **296**, 104–115.

418 Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M. & Jeltsch, F.
419 (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance
420 of keystone structures. *Journal of biogeography*, **31**, 79–92.

421 Tobler, M.W., Carrillo-Percastegui, S.E., Leite Pitman, R., Mares, R. & Powell, G. (2008) An
422 evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest
423 mammals. *Animal Conservation*, **11**, 169–178.

424 Trolle, M. & Kéry, M. (2005) Camera-trap study of ocelot and other secretive mammals in the
425 northern Pantanal. *Mammalia*, **69**, 405–412.

426 Wang, Y. & Fisher, D.O. (2012) Dingoes affect activity of feral cats, but do not exclude them
427 from the habitat of an endangered macropod. *Wildlife Research*, **39**, 611–620.

428