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

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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, 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 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). Cat activity was 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 cats' temporal response to co-occurrences of civets (*Paradoxurus hermaphroditus* and *Viverra tangalunga*) was found but cats in diel activity avoided domestic dogs (*Canis lupus familiaris*). 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.

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3 **habitats on Bohol Island, Philippines**

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26 **Abstract**

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28 species, comprises mainly small- to medium-sized forms with a few large exceptions. As with

29 other tropical ecosystems, the major threats to wildlife are habitat loss, hunting and invasive

30 species, of which the feral cat (*Felis catus*) is considered the most damaging. Our camera-

31 trapping study focused on a terrestrial vertebrate species inventory on Bohol Island and tempo-

32 spatial co-occurrences of feral cats with their prey and competitors. The survey took place in the

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34 agricultural land, and rural areas in the vicinity of villages. Altogether, over 2,885 trap days we

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36 reptile, *Varanus cumingi*. We trapped 81.8% of expected vertebrates. Based on the number of

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39 (Δ=0.62); the lowest was in the same habitat with ground-dwelling birds (Δ=0.40). Cat activity

40 was not recorded inside the rainforest; in other habitats their diel activity pattern differed. The

41 cats' activity declined in daylight in the proximity of humans, while it peaked at the transition

42 zone between rainforest and fields. Both rodents and ground-dwelling birds exhibited a shift in

43 activity levels between sites where cats were present or absent. Rodents tend to become active by

44 day in cat-free habitats. No cats' temporal response to co-occurrences of civets (*Paradoxurus*

45 *hermaphroditus* and *Viverra tangalunga*) was found but cats in diel activity avoided domestic

46 dogs (*Canis lupus familiaris*). Our first insight into the ecology of this invasive predator in the

47   Philippines revealed an avoidance of homogeneous primary rainforest and a tendency to forage

48   close to human settlements in heterogeneous habitats. A detailed further investigation of the

49   composition of the cat's diet, as well as ranging pattern, is still needed.

50   **Introduction**

51   The Philippine Archipelago is considered a global biodiversity hotspot, known for its

52   high proportion of endemic species (Ambal *et al.* 2012). The terrestrial vertebrate taxa, which

53   primarily encompass small to medium sized species, inhabit more than 7100 islands. These

54   species include at least 213 mammals (Heaney *et al.* 2010), 674 birds (Lapage 2015), 270

55   reptiles and 111 amphibians (BREO 2015).

56   Similar to other oceanic islands, the predominantly small fauna of the Philippines suffers

57   from the presence of competing invasive species, such as *Rattus* spp., and the feral cat (*Felis*

58   *catus*). The cat is listed as the most widespread and probably most damaging of the four

59   carnivores included on the list of the 100 worst invasive species (Lowe *et al.* 2000). At least 175

60   vertebrates are threatened or have been driven to extinction by feral cats on at least 120 islands

61   (Medina *et al.* 2011). Meta-analysis has revealed that the negative impact of feral cats is largest

62   for insular endemic mammals, and is exacerbated by the presence of invasive cat prey species

63   such as mice (*Mus musculus*) or rabbits (*Oryctolagus cunuculus*) (Nogales *et al.* 2013). The cat

64   is widely kept as a pet by people throughout the Philippines and can be found foraging in every

65   habitat (Duffy & Capece 2012). Despite the general prevalence of cats in the Philippine

66   landscape, there is a noticeable lack of knowledge regarding the cat's impact on the biodiversity

67   of this archipelago.

68   Cats feed on a wide range of animals, from arthropods, reptiles and birds to mammals the

69   size of a rabbit (Pearre, Maass & Maass 1998). In Australia alone, with a variety of animals of

70   similar size such as those found in the Philippines, 400 prey species consumed by cats have been

71   recorded (Doherty *et al.* 2015). In the Philippines, members of the orders Chiroptera and

72   Rodentia are the most numerous mammalian species (Heaney *et al.* 2010). A wide range of

73   terrestrial and arboreal rodents with body mass ranging from the 15-g *Musseromys* spp. to the

74   2.6-kg *Phloeomys* spp. risk predation by cats. Only adult individuals of *Phloeomys* and *Hystrix*

75   *pumila* (Heaney *et al.* 2010) exceed the potential prey dimensions. According to size and niche,

76   members of the Tupaiidea (treeshrews), Erinaceidae (moonrats) and Soricidae family (shrews)

77   should be listed as mammalian prey for cats. Similarly, the smallest Philippine primate, *Tarsius*

78   *syrichta*, which inhabits Bohol and other islands of the Mindanao faunal region, can be included

79   (MacKinnon & MacKinnon 1980).

80   On Bohol Island (3,269 km^2), as on the other Philippine islands, bats and rodents

81   dominate among local mammals. The small mammalian fauna consists of one insectivorous

82   species and nine species of rodents, including the introduced *Mus musculus, Rattus rattus, Rattus*

83   *norvegicus, Rattus tanezumi* and *Rattus exulans* (Heaney *et al.* 2010). The avifauna of Bohol

84   numbers 235 species, with Passeriformes forming the largest sub-group at 83 species. Bohol is

85   also home to 14 ground-dwelling bird species inhabiting the woody or bushy inland habitats

86   potentially affected by cats (Kennedy 2000).

87   Along with dogs (*Canis lupus familiaris*), possible competitors of cats on Bohol include

88   two mammalian carnivores, Asian palm civet (*Paradoxurus hermaphroditus*) and Malayan civet

89   (*Viverra tangalunga*) (Heaney *et al.* 2010) and two reptile species: yellow-headed water monitor

90   (*Varanus cumingi*) and reticulated python (*Python reticulatus*) (BREO 2015). To our knowledge,

91   no predation between cat and civets has been published.

92   The timing of activity of mammalian predators is a well discussed topic (e.g. Palomares

93   & Caro 1999; Tambling *et al.* 2015). Time-stamped records from camera traps allow for detailed

94   insights into the time budget and temporal coexistence of animals across trophic guilds, seasons,

95   etc. (Rowcliffe *et al.* 2014), and recent camera trapping studies have successfully examined

96   overlaps in diel activity patterns (Ridout & Linkie 2009), confirming significant activity overlap

97   between carnivores and their preferred prey (Harmsen *et al.* 2009; Lucherini *et al.* 2009;

98   Sweitzer & Furnas 2016) and suggesting predator behavior to reduce foraging energy

99   expenditure (Foster *et al.* 2013). In their role as mesopredators cats must optimize their use of

100   time not only to encounter prey but also to cope with a sympatric superior predator (Brook,

101   Johnson & Ritchie 2012). The combination of partitioning of habitat, prey size and a 24-hour

102   daily cycle is thought to be a complex mechanism allowing competing felids to coexist in

103   different animal communities (Di Bitetti *et al.* 2010; Foster *et al.* 2013; Silmi, Anggara & Dahlen

104   2013; Sunarto *et al.* 2015). For example, low overlap in activities has been found between

105   marbled cat (*Pardofelis marmorata*) and clouded leopard (*Neofelis nebulosa*) in Thailand

106   (Lynam *et al.* 2013). Wang & Fisher (2012) also confirmed higher segregation of diel activities

107   of cats with respect to dingoes during wet months. The particularly suppressive effect of an apex

108   carnivore on invasive populations of cats is considered an important conservation issue (Brook,

109   Johnson & Ritchie 2012; Lazenby & Dickman 2013; Doherty, Bengsen & Davis 2015).

110   We conducted a camera-trap survey on Bohol Island in an attempt to uncover tempo-spatial co-

111   occurrences of terrestrial vertebrate species on regularly used trails and to confirm the presence

112   of cats in the protected primary rainforest (Zone I), a transition zone along the border of the

113   primary rainforest with the agricultural landscape (Zone II), and inside the rural landscape in the

114   proximity of human settlements (Zone III). Our objectives were to: (1) create a general inventory

115   of camera-trapped taxa; (2) model the species accumulation curve using previous knowledge of

116   the possible number of mammalian, avian and reptile species detectable by camera-traps; and (3)

117   compare the diel activity levels of cats with those of potential prey and competitors.

118   **Materials & Methods**

119   *Study site*

120   Our study was conducted under research permit No. 2014-04, issued by DENR, Region

121   VII, Philippines, between July 2nd and December 4th, 2014 in the surroundings of the town of

122   Bilar, Bohol Island, Philippines. The landscape consists of a mixture of distinctive flat rural areas

123   near human settlements, used as rice fields and plantations for various crops, steep karst hills

124   covered by brush and secondary forest, and primary rainforest in protected areas. The town of

125   Bilar lies between two conservation areas, the Rajah Sikatuna Protected Landscape (RSPL) and

126   the Loboc River Watershed Forest Reserve. RSPL is the second largest protected sanctuary on

127   Bohol, covering 11,034 ha of a mostly hilly limestone environment rich in characteristic

128   landforms such as ravines, sinkholes and caves. The altitude in RSPL varies between 300 and

129   826 m above sea level. The forest canopy is multi-layered, with trees reaching up to 20 m in

130   height. Members of the families Dipterocarpaceae, Moraceae and Melicacea dominate the

131   canopy. Certain regions of RSPL have been reforested with white teak (*Gmelina arborea*) and

132   Honduras mahogany (*Swietenia macrophylla*) (Barcelona *et al.* 2006). The average annual

133   precipitation reaches 1,600 mm; the rainy season typically lasts from June to December, with an

134   increase in precipitation to 200 mm per month. The driest month is April when approximately 40

135   mm of rain falls.

136   *Sampling design*

137   We monitored three types of landscape typical of tropical regions and deployed cameras

138   in groups, one camera per location, at eight trapping sites (Fig. 1): Zone I – protected primary

139   rainforest including the Watershed Forest Reserve (site WS), interior of RSPL (site SP) and

140   abandoned farms in the early stages of succession into RSPL (site SF); Zone II – transition zone

141   between the primary rainforest of RSPL and rice fields close to the village of Bulak (site BU),

142   transition zone between RSPL and rice and corn fields close to Logarita Springs (site LS), and

143   transition zone between RSPL and the farms of the village Binantay (site BI); Zone III – mixture

144   of brush and degraded forest and plantations on the edge of the village of Subayon (site SU), and

145   at Bohol Habitat Conservation Center on the edge of the town of Bilar (site HB). Details on

146   camera traps' deployment and duration of sampling are shown in Table 1.

147   *Sampling procedures*

148   We used 41 weatherproof infrared digital camera traps – 29 units of Ltl Acorn 5210MC

149   (Shenzhen Ltl Acorn Electronics Co., Ltd.) and 12 units of SPYPOINT IR7 (SPYPOINT[MD], G.G.

150   Telecom). Prior to the study, we tested both types of cameras in a week-long trial which was

151   focused on the difference in detection rates for moving objects. No difference larger than 10 %

152   between numbers of independence events was found. Both types of cameras were also used in

153   every habitat to avoid a bias from site-specific detection rates. Cameras were set up to perform

154   the same delay between recordings – SPYPOINT to take two images with a delay of 10 s

155   between consecutive triggering, and Ltl Acorns to take one picture followed by a 5 s video, with

156   a 5 s delay between triggering. Video sequences served as an additional tool for the identification

157   of species.

158   We placed all cameras opportunistically on the most frequented trails or their junctions

159   and, according to the expected size of target vertebrates, we fastened cameras with a belt onto the

160 trunks of trees or bushes nearest to the trail, at a height of up to 0.5 m, with a focal point

161 approximately 2 m from the lens. All cameras were active 24 hours a day; all records in infrared

162 mode were available only in a black-and-white version. No bait was used.

163 *Identification of taxa*

164   Two observers, VB and TJ, independently identified all species visually from images and

165 videos; the results were mutually crosschecked, and disagreeing or unidentifiable records were

166 excluded from the analysis. Based on available databases (Heaney *et al.* 2010; BREO 2015;

167 Lapage 2015), we made a list of terrestrial mammalian and avian ground-dwelling species

168 known or expected to occur on Bohol (Table 2). From reptiles, we included only the largest four-

169 legged taxon, the yellow-headed water monitor (*Varanus cumingi*). Members of the order

170 Chiroptera and the strictly arboreal Philippine colugo (*Cynocephalus volans*) were *a priori*

171 omitted. The conservation status of each species was assessed following IUCN (2015).

172   Due to the limited nature of the recordings, for the identification process and the

173 calculation of a species accumulation curve all taxa the size of a mouse (*Mus musculus* and also

174 the insectivorous *Crocidura beatus*) were pooled into the group called 'mice', and all species of

175 rats (*Rattus* spp. and *Bullimus bagobus*) into the group 'rats'. In addition, both known species of

176 squirrels (*Exilisciurus concinnus* and *Sundasciurus philippinensis*) were grouped into one taxon:

177 'squirrels'. In total, the list consisted of eight taxa of mammals, 13 birds and one reptile. For

178 purposes of *overlap* analyses between cats and their competitors and prey, we pooled both native

179 carnivore species into a group called 'civets' and put mice, rats and squirrels into the group

180 'rodents'. Ground-dwelling species of birds were the second analyzed group of prey; dogs were

181 accordingly examined as competitors.

182 *Data analysis*

183   Photographs were defined as events (or activity records) when the delay between two

184   consecutive images of an individual exceeded 10 min. The same individual could theoretically

185   trigger more than one camera within 10 min. For each species and Zone, in Table 2 we reported

186   occurrences of species at cameras represented by events (Lazenby & Dickman 2013).

187   We used a species accumulation curve based on the cumulative number of camera-

188   trapping days, computed in EstimateS Version 9.1.0 (Colwell 2013), to find out if our survey

189   lasted a sufficient number of days to capture the 22 expected terrestrial vertebrate species

190   (including three pooled groups) known from Bohol. We followed Tobler *et al.* (2008) and

191   calculated well-performing estimators of species richness: the non-parametric abundance-based

192   estimator ACE, and the non-parametric incidence-based estimators ICE and Jackknife 1. An

193   abundance-based rarefaction approach with 95% confidence intervals and 1,000 random

194   iterations of sample order was used.

195   The pair-wise temporal overlap of selected activity patterns was analyzed using the R

196   statistical environment package '*overlap*' (Meredith & Ridout 2014). Following Ridout and

197   Linkie (2009), we applied kernel density estimation on circular data pooled within all study sites.

198   Density of activity (y-axis) uses a von Mises kernel, corresponding to a circular distribution, and

199   is based on recorded time of each event on 24-hour x-axis. The coefficient of overlap (Δ) was

200   calculated with a smoothing parameter of 1.0. We used a smoothed bootstrap of 10,000

201   resamples to determine standard errors and 95% confidence intervals. We only analyzed

202   combinations of pairs of species, which scored at least 30 events in the activity record (Ridout,

203   pers. comm.) in a given environment. The number of events used for calculation of the activity

204   pattern overlap for each analyzed group of animals and each location is shown in Table 3.

205   **Results**

206   *Species inventory*

207   During the whole survey period, lasting 155 days, we accumulated 2,885 trap days and

208   2,034 events. The combined capture rate across all sites was 73.1 events per 100 trap days. The

209   list of all 30 animal taxa recorded is shown in Table 2.

210   The most frequent native species was the barred rail (*Gallirallus torquatus*), captured in 183

211   independence events. We did not record four expected bird species: *Megapodius cumingii,*

212   *Coturnix chinensis, Turnix sylvaticus* and *Gallinago megala.* On the other hand, we confirmed

213   the survival of the Philippine warty pig (*Sus philippensis*). Given its size, it was probably a male

214   individual that was captured, only once, on three images on August 9th (6:35 pm) in a mud

215   wallow in the interior of RSPL.

216   We found that feral cats most often occurred in the Zone II and III, and were absent

217   inside the primary forest. A similar trend was found for ground-dwelling birds. Most rats and

218   other small mammals were recorded in the transition Zone II between the RSPL forest and

219   agricultural land. Along with feral cats and domestic dogs, we also recorded all three medium-

220   sized mammals occurring on Bohol – the common palm civet (59 events), Malay civet (16

221   events) and long-tailed macaque (*Macaca fascicularis*) (7 events). Humans were also captured

222   but excluded from the analysis.

223   Within all eight sampling sites, we captured 18 of 22 expected target taxa, which

224   corresponds to a success rate of 81.8% of the species inventory (100% of mammals and reptiles,

225   69.2% of birds). We used these 18 taxa for calculating the species accumulation curve (Fig. 2).

226   The mean estimated species richness computed in EstimateS was 19.7 species (ACE = 19.6, ICE

227   = 19.5 and Jackknife 1 = 20.0). We recorded 15.89 species (72.2% of expected species) in 1,000

228   trap days. The eight target species of mammals were captured in 1,723 trap days; similarly, nine

229   ground-dwelling birds were recorded within 1,435 trap days.

230   *Temporal overlaps*

231   We recorded cats only in transition Zone II and in the rural landscape close to human

232   settlements (Zone III). Diel activity patterns of cats differed among zones (Fig. 3). Cats showed

233   a decrease in late-afternoon activity near villages, whereas activity in the transition area peaked

234   right before noon. Generally, the activity of cats by daylight was higher in transition zones; in

235   Zone III cats were recorded mainly at night.

236   The highest overlap in activity patterns between cats and rodents (Table 4) was found in

237   the rural landscape of Zone III, and between cats and ground-dwelling birds in transition Zone II

238   (Fig. 4).

239   Both categories of potential prey showed shifts in temporal occurrence within sites, based

240   on the presence of cat (Fig. 5). As seen, the peaks of rodent activity decreased in the hours before

241   sunrise and increased after sunset, whereas the activity of ground-dwelling birds peaked about 4

242   hours sooner at sites where cats were not recorded.

243   Cats showed the second lowest overlap among all groups with dogs in Zone III (Table 4)

244   where dogs were dominant and active during the day. In Zone II these two animals appeared to

245   peak in their activity at different times: dogs were most active in the morning and late afternoon,

246   whereas cats peaked before noon (Fig. 4).

247   The overlap between the diel activity patterns of cats and both species of civets is shown

248   in Figure 6. Cats exhibited roughly consistent activity throughout a 24-hour period, with no

249   apparent shift caused by the nocturnal occurrence of sympatric civets.

250   **Discussion**

251   According to our knowledge, to date no study of the behavior and ecology of feral cats

252   has been conducted in the Philippines, nor any camera-trap-based species inventory on Bohol.

253   With the exception of the Philippine pygmy squirrel, *Exilisciurus concinnus*, we were able to

254   capture and identify every non-volant mammalian species recorded as occurring on Bohol larger

255   than a mouse, including an individual of *Sus philippensis*, which is considered to be close to

256   extinction (Oliver 1993), even by local people. Camera traps captured 81.8% of known ground-

257   dwelling mammalian, avian, and reptilian species, similar to the 86 % captured in the Amazon

258   rain forest (Tobler *et al.* 2008) or 89% in the lowland rainforest of Borneo (Bernard *et al.* 2013);

259   both those camera-trapping studies were restricted to mammals. In addition, the initially steep

260   shape of our general species accumulation curve corresponds with studies conducted in tropical

261   ecosystems and confirms the robustness of the approach. Similarly to Rovero *et al.* (2014), we

262   captured the majority of selected species in 1,000 trap days, considered a reliable threshold

263   enabling the detection of rare species (O'Brien 2011).

264   The absence of cats in the interior of primary rainforest seems not to be driven by

265   distance from the nearest human settlements, given that all three monitored sites were up to

266   approximately 3 km from houses. We suggest that the absence of preferred features and habitats

267   in the rain forest may have resulted in camera traps failing to capture cats. Cats typically use a

268   mixture of vegetation cover at ground level which provides both cover and open space for

269   observing their prey; such habitat may increase hunting success (Doherty, Bengsen & Davis

270   2015). The habitat heterogeneity hypothesis by Tews *et al.* (2004) predicts that heterogeneous

271   habitats offer a greater diversity and density of potential prey than homogeneous ones, which

272   could be conceivable for cats. Linear features in space (e.g. tree lines, roads and other corridors)

273   are generally considered to maximize cat's detectability (Crooks 2002; Bengsen, Butler &

274 Masters 2012). We would expect to record cats in primary forest mostly on trails (Trolle & Kéry

275 2005; Harmsen et al. 2010; Anile et al. 2014) but they could disperse into the undergrowth on

276 paths that are undetected.

277 The presence of competing, potentially dangerous predators in primary forest is unlikely

278 to explain the absence of cats. Dogs and both species of civets were equally present in all three

279 zones. The common palm civet and Malay civet are omnivorous with a distinctive nocturnal

280 activity pattern (Jennings *et al.* 2009) but they forage in the habitat of cats, and given their size

281 we consider them to be competitors of cats. Nonetheless, cats do not show any temporal

282 avoidance, indicating no interspecies competition, which has evolved during almost a 500-year

283 co-existence (Jubair 1999). For a more comprehensive view of possible niche partitioning, as

284 found for example between felids on Sumatra (Sunarto *et al.* 2015), a camera-trapping study

285 should be conducted on Negros, where the Visayan leopard cat (*Prionailurus bengalensis* ssp.

286 *rabori*) occurs as a regional direct competitor (IUCN 2015).

287 Our results (Tables 2 and 3) show that species richness and availability of both prey

288 categories (rodents and birds) was higher, nearly by orders of magnitude, in both human-altered

289 zones than in primary rainforest. We attribute this to the variety of vertebrate and invertebrate

290 prey, which is more abundant in heterogeneous landscapes. In addition, as suggested by Lozano

291 *et al.* (2003), feral cats use a wide range of habitat components to meet their different activity

292 requirements (e.g. hunting, resting), and this landscape offers a mixture of agricultural features

293 with secondary growth, infrastructure and potential human subsidies (Ferreira et al. 2011). Our

294 data clearly support such a tendency to forage relatively close to human settlements, however we

295 were not able to determine from our records whether a photographed animal was feral or

296 domestic.

297   Although the diel activity pattern of cats was roughly consistent over 24-h periods (Fig.

298   6), a detailed analysis of zones revealed a decline in diurnal activity in the vicinity of villages, in

299   contrast to an apparent activity peak before noon in Zone II (Fig. 3). Both Zones II and III

300   offered more-or-less the same number of prey species (Table 2). Compared with Zone II, we

301   hypothesize that more uniform diurnal activity of relatively abundant dogs dissuaded cats from

302   daytime foraging in Zone III (Fig. 4). Also subsidies provided by humans in villages could

303   influence cats to remain inactive in shelters and forage at night. We did not detect any sign of

304   cats being spatially excluded by dogs, but our results support findings that cats optimize their

305   timing of hunting behavior to when dogs are less active, hence avoiding potentially dangerous

306   encounters (Brook, Johnson & Ritchie 2012; Wang & Fisher 2012). Cats were more diurnal in

307   Zone II. This could be explained by the same factor, because the zone-specific relative

308   abundance index of dogs was two times lower than the index of cats than in Zone III (Table 3).

309   So cats could respond both to lower disturbance from dogs and to higher diurnal availability of

310   rodents in Zone II (Fig. 4). Other prey not detected by cameras such as insects or lizards might

311   also be present (Bonnaud et al. 2011).

312   Prey species showed shifts in diel activity patterns between sites where cats were, or were

313   not, present (Fig. 5). When cats were absent, rodents tended to forage visibly by day, while the

314   activity of ground-dwelling birds peaked about 4 hours later. It is difficult to interpret the shift in

315   bird activity; data from sites without cats were considered too scarce to perform a reliable

316   analysis. Rodents shift their activities to become nocturnal if cats are present and more diurnal

317   (Doherty et al. 2015). This raised the question of whether almost 500 years of cat presence in the

318   Philippines has driven adaptive mechanisms of prey and competitors to cope with a new predator

319   or not. Our results suggest that this already happened, similarly to the 4000-year history of the

320 dingo in Australia (Carthey & Banks 2012). Nevertheless, we believe that further research is

321 needed, especially throughout all seasons.

322   Knowledge of feral cat diet is paradoxically the least researched in tropical habitats with

323 the richest terrestrial biodiversity (Doherty *et al.* 2015; Doherty, Bengsen & Davis 2015). Our

324 findings reveal the first tempo-spatial co-occurrences between feral cats and their potential prey

325 in a typical mixture of Philippine landscapes. We suggest feral cats' temporal avoidance of dogs

326 as the apex predator. We confirm that camera traps are capable of capturing small-bodied fauna,

327 ground-dwelling birds and highly elusive species, such as *Sus philippensis*, as well. Endangered

328 Philippine fauna exposed to invasive species should rapidly become the target of a broad and

329 long-term camera-trapping inventory survey. For an in-depth knowledge of the dietary intake of

330 feral cats in the Philippines, DNA analysis of scat is recommended as a priority for researchers

331 (Nogales *et al.* 2013). In addition, collared and GPS-tracked cats would provide information

332 about habitat use and the size of home ranges. Finally, attention should be paid to the cultural

333 value of cats kept as pets within Philippine society, to inform eradication strategies.

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464

Figure 1

Schematized map of the study area in the municipality of Bilar

Figure 1. Schematized map of the study area in the municipality of Bilar, Bohol, Philippines. Circles highlight eight sites surveyed from July to December 2014.

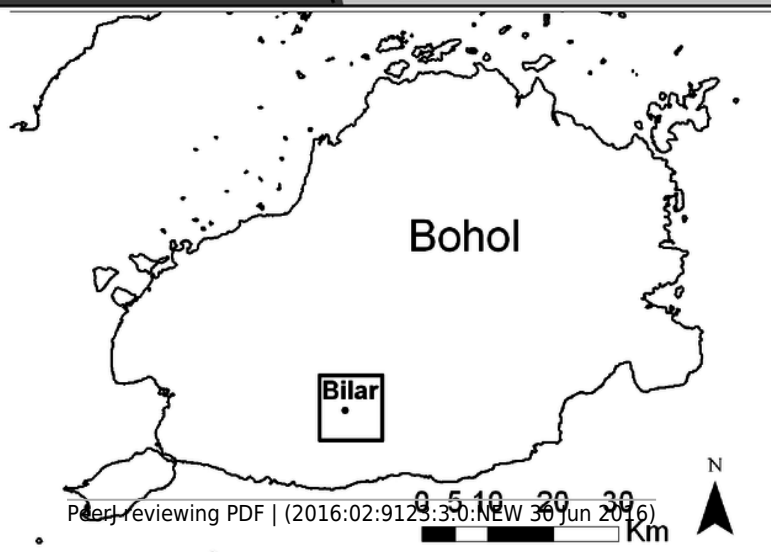
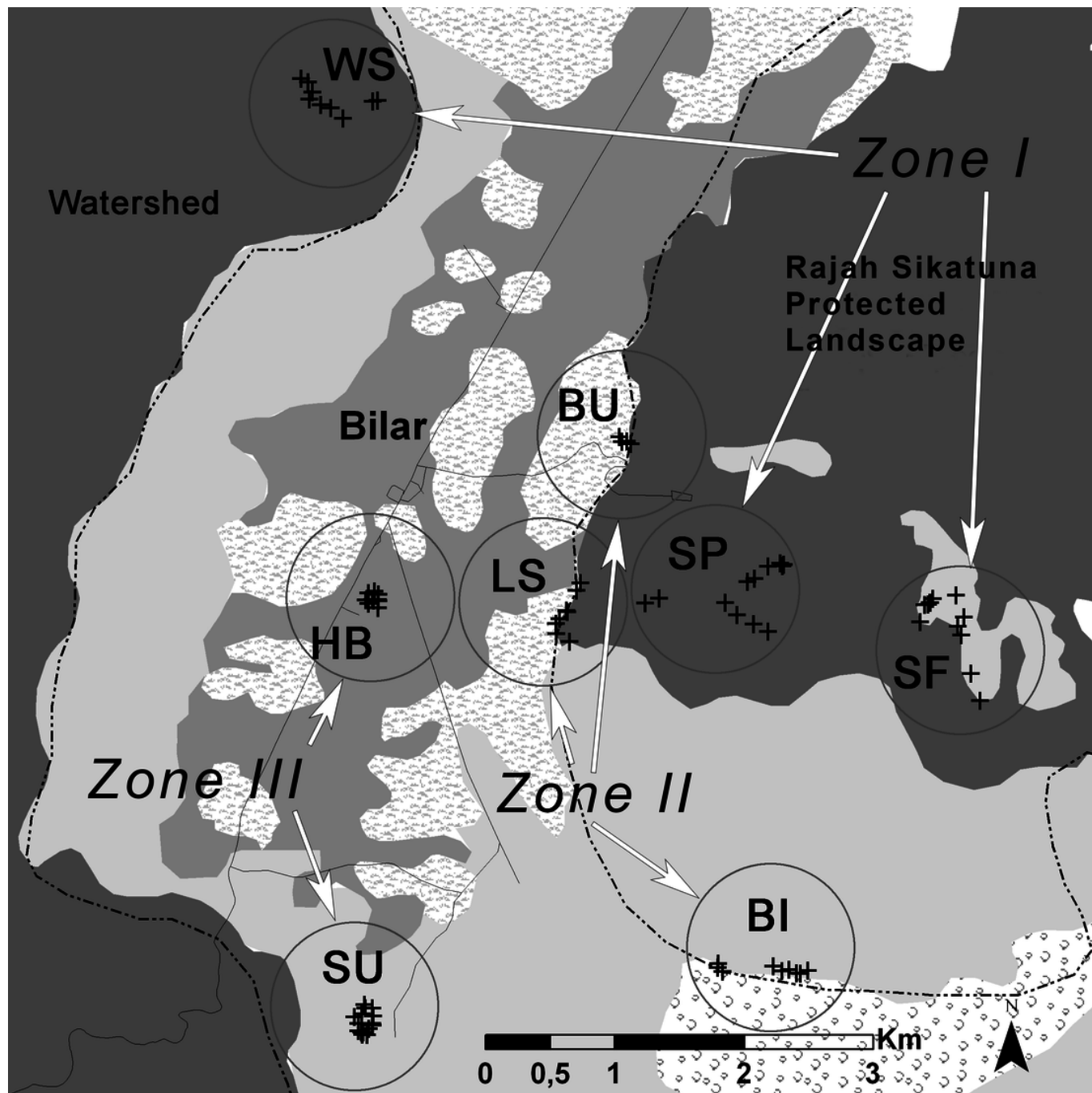



Figure 2

The species accumulation curves with 95% CIs for species captured in all categories of environment in 2,885 trap days

Figure 2. The species accumulation curves with 95% CIs for species captured in all categories of environment in 2,885 trap days. The dashed-and-dotted line marks the known number of species, while the dotted lines represent species richness estimated by Jackknife 1 in EstimateS (Colwell 2013) .

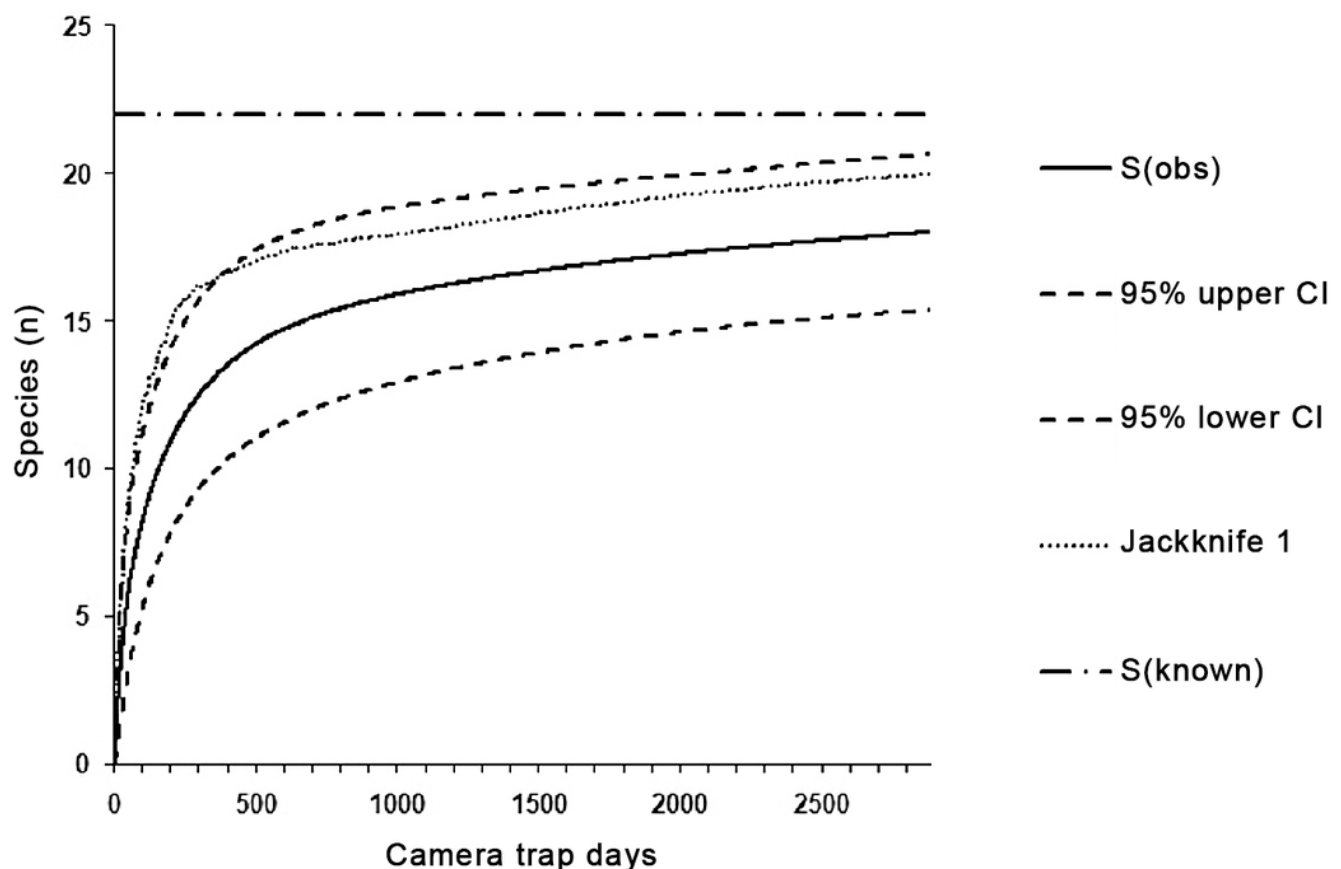



Figure 3

Overlap between diel activity patterns of cats in transition Zone II and rural Zone III

Figure 3. Overlap between diel activity patterns of cats in transition Zone II (dashed line) and rural Zone III. The number represents the coefficient of overlap (Δ), with standard error in parentheses.

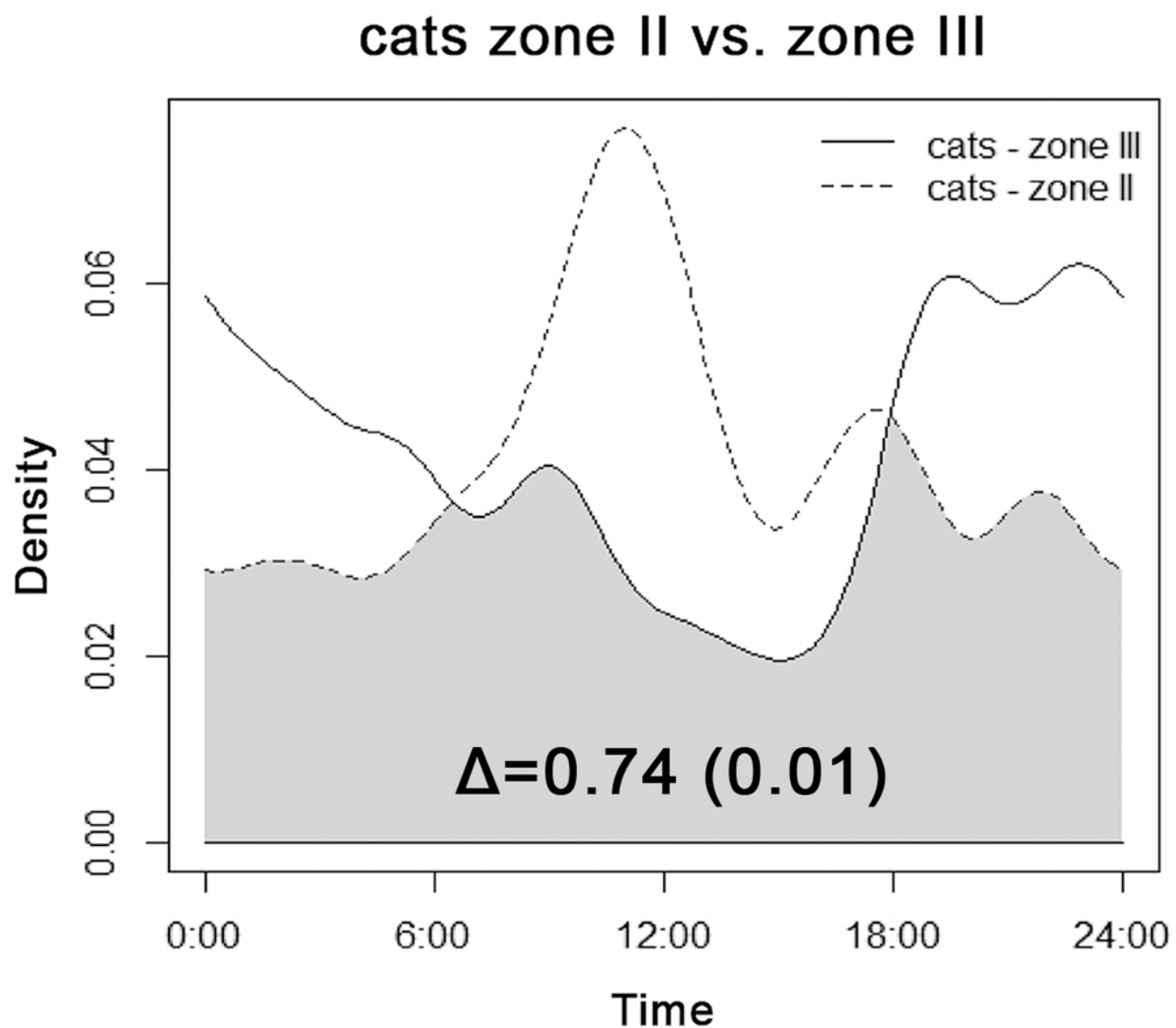



Figure 4

Overlap between the diel activity patterns of cats, rodents, ground-dwelling birds and dogs.

Figure 4. Overlap between the diel activity patterns of cats, rodents, ground-dwelling birds and dogs in transition Zone II (left) and rural Zone III.

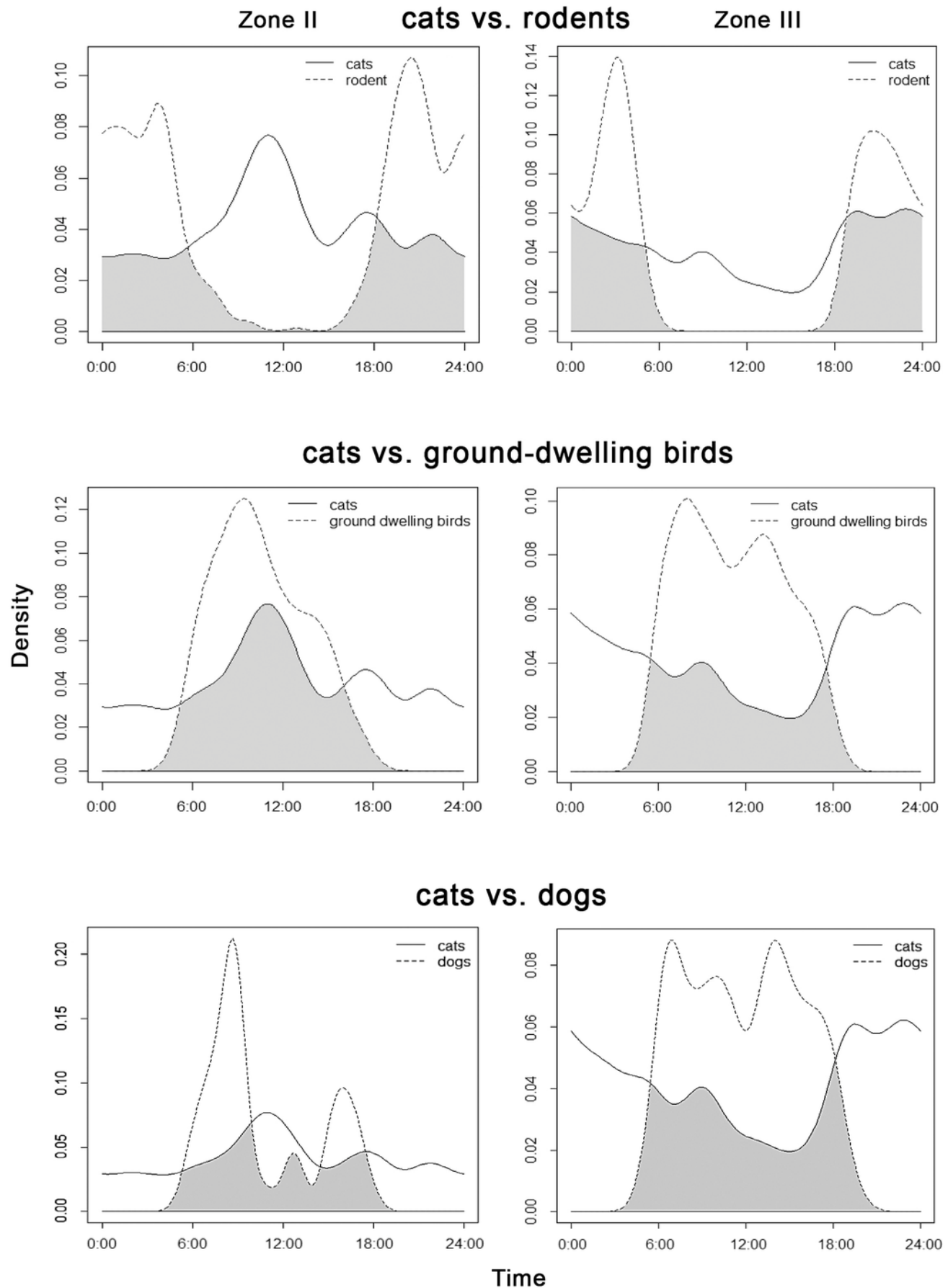



Figure 5

Overlap between the diel activity patterns of rodents and ground-dwelling birds at sites with and without the presence of cats

Figure 5. Overlap between the diel activity patterns of rodents (left) and ground-dwelling birds at sites with and without the presence of cats. The numbers represent coefficients of overlap (Δ) with standard errors in parentheses. Arrows indicate shifts in activity levels if cats are present.

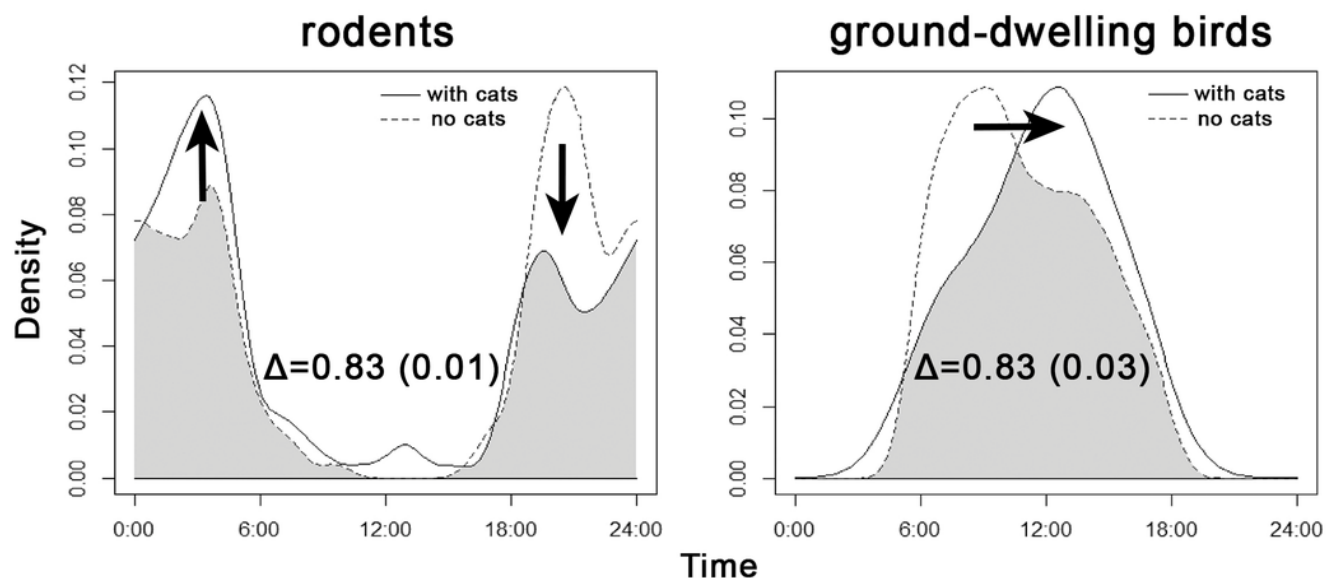



Figure 6

Overlap between the diel activity patterns of cats and both species of civets at all sites

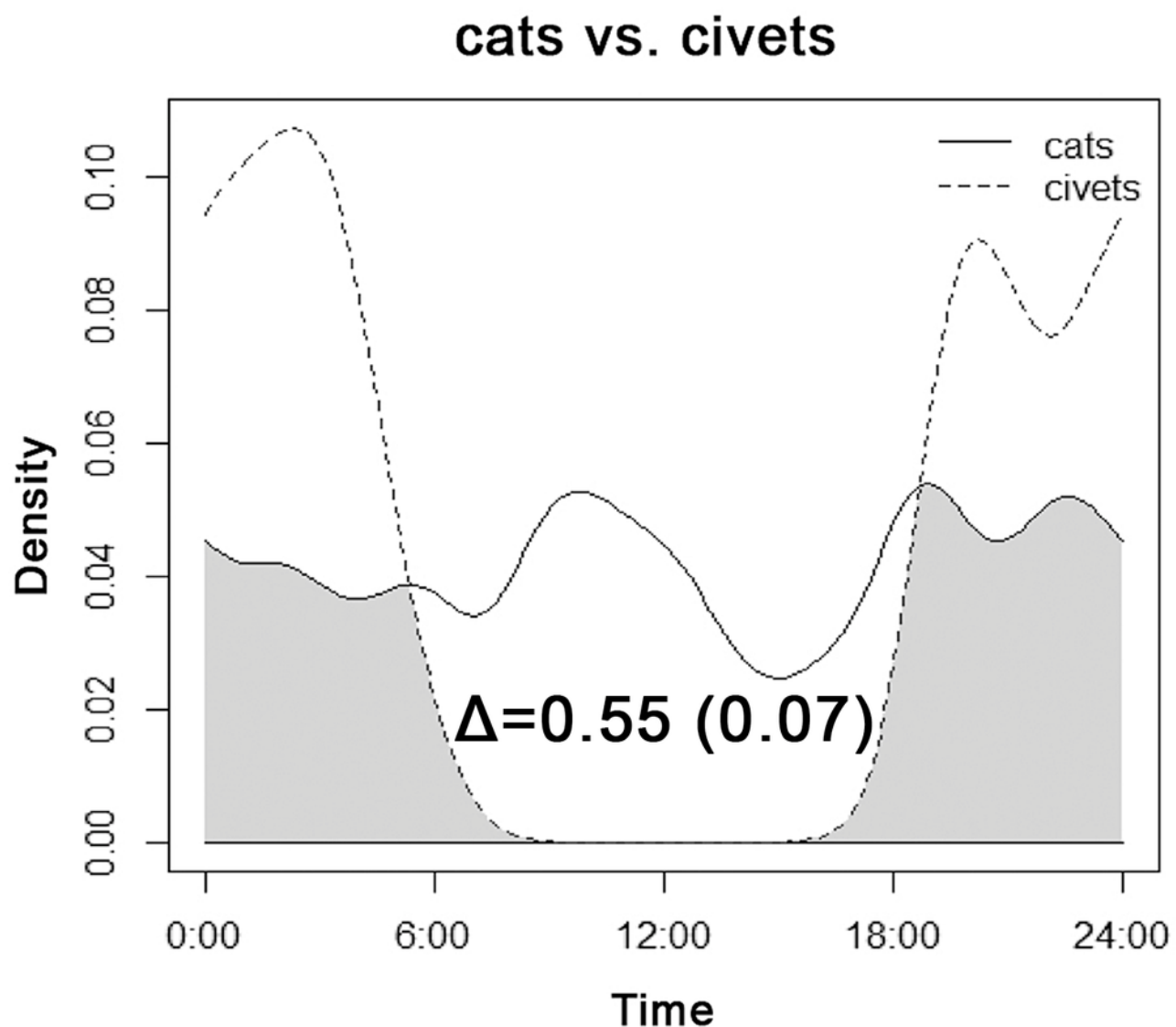
Figure 6. Overlap between the diel activity patterns of cats and both species of civets at all sites of their occurrence.

Summary of the camera trap deployment

Table 1. Summary of the camera trap deployment in the area of the Rajah Sikatuna Protected Landscape, Bohol, Philippines.

1 Table 1. Summary of the camera trap deployment in the area of the Rajah Sikatuna Protected

2 Landscape, Bohol, Philippines.

Zone	Site	Date	*n* camera traps	*n* trap- days	Range of distances between traps (m)
I	SP	12.7. - 30.7. 2014	12	204	60 – 514
I	SF	30.7. - 14.8. 2014	12	173	38 – 307
I	WS	1.8. - 15.8. 2014	9	125	37 – 265
II	BI	2.8. - 4.12. 2014	10	850	28 – 395
II	LS	12.7. - 4.12. 2014	7	536	48 – 174
II	BU	2.8. - 4.12. 2014	4	383	38 – 44
III	HB	5.7. - 31.7. 2014	10	224	25 – 236
III	SU	2.7. - 31.7. 2014	16	390	23 – 139

List of species recorded during a survey in the area of the Rajah Sikatuna Protected Landscape, Bohol, Philippines.

Table 2. List of species recorded during a survey in the area of the Rajah Sikatuna Protected Landscape, Bohol, Philippines. Species denoted with '*' are those expected for the species accumulation curve. Values represent number of events of species recorded in each zone.

1 Table 2. List of species recorded during a survey in the area of the Rajah Sikatuna Protected

2 Landscape, Bohol, Philippines. Species denoted with '*' are those expected for the species

3 accumulation curve. Values represent number of events of species recorded in each zone.

Common name	Scientific name	Zone I	Zone II	Zone III	Site
Philippine warty pig*	*Sus philippensis*	1	0	0	SF
Common palm civet*	*Paradoxurus hermaphroditus*	10	43	6	Su,Bi,LS,Bu,SP,SF,Ws
Malay civet*	*Viverra tangalunga*	1	8	7	Ha,Bi,LS,SP
Long-tailed macaque*	*Macaca fascicularis*	3	4	0	LS,Bu,Ws
Philippine tarsier*	*Tarsius syrichta*	0	1	2	Su,LS
Philippine tree squirrel*	*Sundasciurus philippinensis*	4	42	1	Su,LS,Bu,SP,SF,Ws
Dog	*Canis lupus familiaris*	14	39	91	Su,Ha,Bi,LS,Bu,SP
Cat	*Felis catus*	0	97	83	Su,Ha,Bi,LS
Rat*	*Rattus* spp.	32	242	47	Su,Ha,Bi,LS,Bu,SP,SF,Ws
Mice*	*Mus* spp.	5	217	5	Su,Ha,Bi,LS,Bu,SP,SF,Ws
Yellow-headed water monitor*	*Varanus cumingi*	1	6	5	Su,LS,SF
Hooded pitta*	*Pitta sordida*	0	0	41	Ha
Red-bellied pitta*	*Pitta erythrogaster*	0	42	0	Bi,LS
Azure-breasted pitta*	Pitta steerii	1	0	0	Ws
Striated wren-babbler*	*Ptilocichla mindanensis*	1	9	0	LS,Ws
Red junglefowl*	*Gallus gallus*	0	5	14	Su,LS,Bu
Barred rail*	*Gallirallus torquatus*	0	4	179	Su,Ha,Bi,LS,Bu
Slaty-legged crake*	*Rallina eurizonoides*	0	0	15	Su,Ha
Ruddy-breasted crake*	*Zapornia fusca*	0	2	1	Su,Bu
Plain bush-hen*	*Amaurornis olivacea*	0	0	10	Su
Black-faced coucal	*Centropus melanops*	2	4	2	Su,Bi,LS,Bu,SF,Ws
Philippine coucal	*Centropus viridis*	0	2	3	Su,Bu
Emerald dove	*Chalcophaps indica*	7	7	16	Su,Ha,Bi,LS,Bu,SF,Ws
Philippine magpie-robin	*Copsychus mindanensis*	0	3	1	Ha,Bi
Mindanao bleeding-heart	*Gallicolumba crinigera*	1	2	0	LS,SP
Hair-crested drongo	*Dicrurus hottentottus*	1	0	0	SF
Besra	*Accipiter virgatus*	0	1	1	Su,Bi
Philippine hawk-owl	*Ninox philippensis*	0	0	1	Ha
Yellow-breasted tailorbird	*Orthotomus samarensis*	0	1	0	Bi
Domestic chicken	*Gallus gallus domeaticus*	10	254	9	Su,Bi,LS,Bu,SP,SF

Number of independent events used for calculation of activity pattern overlap for each analyzed group of animals and each location

Table 3. Number of events used for calculation of activity pattern overlap for each analyzed group of animals and each location in the area of the Rajah Sikatuna Protected Landscape, Bohol, Philippines. Values in parentheses show the zone-specific relative abundance index (events/total trap days in zone*100). Dashes denote unprocessed entries.

1   Table 3. Number of events used for calculation of activity pattern overlap for each analyzed

2   group of animals and each location in the area of the Rajah Sikatuna Protected Landscape,

3   Bohol, Philippines. Values in parentheses show the zone-specific relative abundance index

4   (events/total trap days in zone*100). Dashes denote unprocessed entries.

	Zone I	Zone II	Zone III	All sites	no cats	with cats
cats	0 (0)	67 (4.57)	83 (13.52)	150 (5.81)	-	-
dogs	14 (2.79)	37 (2.53)	90 (14.66)	141 (5.46)	-	-
rodents	41 (8.17)	480 (32.76)	47 (7.65)	568 (22.00)	41 (8.18)	527 (25.35)
ground-dwelling birds	12 (2.39)	242 (16.52)	263 (42.83)	517 (20.03)	12 (2.39)	505 (24.29)
civets	11 (2.19)	16 (1.09)	13 (2.12)	40 (1.39)	-	-

Activity pattern overlaps between cats, their potential prey and competitors in transition Zone II, rural Zone III and among all sites surveyed in the area of Bilar

Table 4. Activity pattern overlaps between cats, their potential prey (rodents and ground-dwelling birds) and competitors (dogs and civets) in transition Zone II, rural Zone III and among all sites surveyed in the area of the Rajah Sikatuna Protected Landscape, Bohol, Philippines.

1 Table 4. Activity pattern overlaps between cats, their potential prey (rodents and ground-

2 dwelling birds) and competitors (dogs and civets) in transition Zone II, rural Zone III and among

3 all sites surveyed in the area of the Rajah Sikatuna Protected Landscape, Bohol, Philippines.

	site	overlap (Δ)	*SE*	95% l*CI*	95% u*CI*
cats vs. rodents	Zone II	0.48	0.023	0.37	0.58
	Zone III	0.62	0.002	0.52	0.73
cats vs. ground-dwelling birds	Zone II	0.61	0.019	0.50	0.71
	Zone III	0.40	0.041	0.30	0.50
cats vs. dogs	Zone II	0.50	0.052	0.36	0.62
	Zone III	0.45	0.041	0.35	0.56
cats vs. civets	All sites	0.55	0.067	0.45	0.64