Andrew P. Jennings*, John Mathai, Jedediah Brodie, Anthony J. Giordano and Geraldine Veron **Predicted distributions and conservation status of** two threatened Southeast Asian small carnivores: the banded civet and Hose's civet

Abstract: Knowledge of the distribution and habitat preferences of a species is of paramount importance when assessing its conservation status. We used accurately recorded occurrence records and ecological niche modelling to predict the distribution of two threatened and poorly known small carnivore species that occur in Southeast Asia, the banded civet (Hemigalus derbyanus) and Hose's civet (Diplogale hosei), and analysed their spatial niche differentiation for habitat and elevation. We then identified possible anthropogenic threats, and used our modelling predictions to recommend surveying priorities. The predicted distribution of the banded civet was principally in lowland evergreen forest in southern Myanmar/Thailand, Peninsular Malaysia, Sumatra, Borneo and three Mentawai Islands (Siberut, Sipora and South Pagai), and for Hose's civet in evergreen forest across the higher elevation regions of Borneo. Our niche analyses suggested that there is a tendency for these two species to separate spatially along an elevation gradient: the banded civet is mainly found in lowland areas, whereas Hose's civet primarily occurs at higher elevations. Our study strongly indicated that these two viverrids are forest-dependent species that may be threatened by forest loss, degradation and fragmentation. Field surveys should be prioritised in areas where each species is predicted to occur and no records currently exist.

Keywords: *Diplogale hosei*; ecological niche; *Hemigalus derbyanus*; Maxent; Viverridae.

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Introduction

Knowledge of geographical distributions and habitat preferences is central to the conservation of threatened species and is of paramount importance when assessing their conservation status and evaluating levels of threats and protection (Thorn et al. 2009, Jackson and Robertson 2011, Rondinini et al. 2011). Presence-only ecological niche modelling (ENM) can be a useful tool for predicting the distributions of poorly known species in remote and inaccessible regions (Gaubert et al. 2006, Papes and Gaubert 2007, Wilting et al. 2010, Jennings and Veron 2011, Jenks et al. 2012). The outputs of ENM can aid conservation planning by highlighting potential unknown populations and key areas for fieldwork and conservation initiatives (Peterson 2006, Thorn et al. 2009, Jackson and Robertson 2011). ENM uses the environmental characteristics of known distribution points to assess the suitability of regions where currently no records of a species exist (Elith et al. 2006). Though presence-only models may potentially generate biased predictions (Phillips et al. 2009), Gormley et al. (2011) have shown that these methods can generate very similar predicted distributions to those that use occupancy modelling and observed presence-absence data.

Although the lack of species records from regions of predicted presence can be simply an artefact of inadequate sampling effort, unoccupied areas might highlight instances where other factors, such as biogeographical and ecological barriers or interspecific competition, have played a role in restricting the range of a species (Phillips et al. 2006, Jennings and Veron 2011). Species persistence in predicted areas may also be influenced by humaninduced factors, such as habitat loss and hunting (Corlett 2007, Thorn et al. 2009). Thus, identifying and assessing the level of anthropogenic threats is vital for developing conservation strategies.

The banded civet *Hemigalus derbyanus* (Gray, 1837) and Hose's civet *Diplogale hosei* (Thomas, 1892) are two closely related small carnivore species within the subfamily Hemigalinae, Viverridae (Veron 2010, Wilting and Fickel 2012) that occur within Southeast Asia (Jennings and Veron 2009). Both species have long slender bodies

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and weigh between 1 and 3 kg. The banded civet is buffygrey to reddish brown, with dark stripes along the face, across the back and around the base of the tail, and Hose's civet has a dark brown to blackish coat with white underparts (Jennings and Veron 2009). Camera-trapping data and sightings suggest that both species are nocturnal and solitary (Van Rompaey and Azlan 2004, Jennings and Veron 2009, Mathai et al. 2010, Brodie and Giordano 2011, Matsubayashi et al. 2011, Samejima and Semiadi 2012), but very little is known about their distribution patterns, habitat preferences and conservation status. Both species are a high conservation priority (Schreiber et al. 1989) and are currently classified as 'Vulnerable' (IUCN 2012).

In this study, we produced distributional and ecological niche information for the banded civet and Hose's civet, and used this to discuss their conservation status. Using Maxent ENM software (Phillips et al. 2006; http:// www.cs.princeton.edu/~schapire/maxent/), we predicted the distributions of these two viverrids by combining accurately recorded occurrence data with two environmental variables, habitat and elevation, that have key distribution and conservation implications for mammal species (Catullo et al. 2008, DeMatteo and Loiselle 2008, Brito et al. 2009, Jennings and Veron 2011, Rondinini and Boitani 2012). Maxent has been shown to perform better than other ENM approaches (Elith et al. 2006), especially with low numbers of occurrence data (Papes and Gaubert 2007, Pearson et al. 2007), and it also produces continuous suitability estimates that are useful for indicating high priority areas for surveying and conservation planning (DeMatteo and Loiselle 2008, Wilting et al. 2010). We also examined the habitat and elevation preferences of each civet species and analysed their niche overlaps for these two variables. Using our modelling predictions and niche analyses as well as current knowledge of civet species, we identified and assessed possible anthropogenic threats and made recommendations for surveying priorities.

Materials and methods

Occurrence data

In addition to our data (Mathai et al. 2010, Brodie and Giordano 2011; unpublished camera-trap data collected from Borneo, 2011–2012), we compiled different types of occurrence records (camera-trap detections, sightings, trappings and specimens) from many sources. Out of 30 researchers who had provided unpublished small carnivore records from Southeast Asia, 19 had records of the

banded civet and/or Hose's civet from their study site (see Acknowledgments). An extensive search of the literature was undertaken to gather published records (63 references). The location details of 295 museum specimens were collected from 31 museums during personal visits or obtained from curators and online databases. Further information concerning the occurrence data set is available upon request from the authors.

Although it was not possible to control for any spatial differences in surveying and collection efforts, we lessened any potential biases in the occurrence data set by compiling information from many independent studies (in all types of habitats and across a wide geographical area and a broad range of elevations). The issue of biased occurrence data is inherent in all ENM studies that use records collected non-systematically across a region (Phillips et al. 2006, Phillips et al. 2009), so the findings from these studies should be interpreted with caution. We georeferenced records with only described localities using Global Gazetteer v 2.1 (www.fallingrain.com/world/). To ensure that all the records were independent, and to minimize the effects of spatial autocorrelation on the modelling analyses, additional records from the same exact location or within 1 km were not used (Wilting et al. 2010). Specimen records from museum databases and publications were crosschecked to eliminate any duplicates. Although it was not possible to double-check all the occurrence data, we personally verified 40% of the camera-trap photographs and 60% of the museum specimens and investigated the validity of outlier records. After processing the raw data set (655 records: 568 for Hemigalus derbyanus and 87 for Diplogale hosei), a total of 254 independent records were used in the analyses (Table 1).

All records were given an accuracy code (AC 1 to AC 4; Jennings and Veron 2011) based on the precision of the location: AC 1, location recorded using a GPS unit (e.g., camera-trap detections); AC 2, location determined using accurate maps and detailed field information (e.g., sightings); AC 3, only a description of the locality recorded (e.g., museum specimens); and AC 4, reported record (no details of type of record or precise coordinates). The precision of AC 1 and AC 2 records was less than ± 250 m and up to several km for AC 3 and AC 4 records.

Ecological niche modelling

The extent of occurrence of the banded civet was determined using the outermost records for this species; for Hose's civet, we assumed that the coastline of Borneo demarcated the outermost limits of its distribution as

Species	Type of record	AC 1	AC 2	Date range AC 1 and AC 2	AC 3	AC 4	Date range AC 3 and AC 4	Hab+Elv model n=AC 1+AC 2
Hemigalus derbyanus	Camera-trap	106	7	1999–2012	1	0	2011	119
	Specimen	0	0	-	84	0	1838-2009	
	Sighting	3	3	1990-2008	10	0	1986-2005	
	Reported	0	0	-	0	1	-	
Diplogale hosei	Camera-trap	22	1	2004-2012	0	0	-	27
	Specimen	0	0	-	12	0	1891-1962	
	Sighting	0	2	1991-2002	0	0	-	
	Тгар	0	2	1983–1997	0	0	-	

 Table 1
 Number and type of independent records within each accuracy category (AC 1 to AC 4), date ranges for records [(AC 1 and AC 2) and (AC 3 and AC 4)] and n-values for habitat+elevation (Hab+Elv) modelling and niche analyses.

AC 1=exact location recorded using a GPS unit; AC 2=exact location determined using accurate maps/information; AC 3=only a description of the locality recorded; AC 4=reported records.

this species has only been recorded on this island (Jennings and Veron 2009). Within these distribution limits, two environmental GIS layers, habitat and elevation, were combined with the occurrence data to predict the areas of occupancy with respect to these two variables, as in Jennings and Veron (2011). We used a 2010 land cover map (250-m resolution) for Southeast Asia (http:// www.eorc.jaxa.jp/SAFE/LC MAP/; Miettinen et al. 2012) that was reclassified to eight cover classes (evergreen forest, peatswamp forest, mangrove, plantation, mosaic, open areas, water and urban). A digital elevation model (1-km resolution) was used as an elevation layer (www.ngdc.noaa.gov/mgg/topo/gltiles.html; tiles H and L) and projected in ArcView GIS 3.3 (ESRI, Redlands, CA, USA) as 300-m bandwidths. We used only records AC 1 and AC 2 for the distribution modelling, as the precision of each locality was within the resolution of both GIS layers, and 97% of these records were within ± 11 years of the habitat layer (see Table 1 for date ranges and n values). For each species, the environmental layers were clipped to the extent of occurrence, resampled to the same cell size (0.0083 decimal degrees) and then entered with the occurrence data into Maxent 3.3.3k (www.cs.princeton.edu/~schapire/maxent). This program was run with the 'auto features' option checked and all other parameters at their default settings (Phillips and Dudik 2008). A jacknife analysis was conducted to measure variable importance. The area under the curve (AUC) of the receiver operating characteristic plot was used as a measure of model performance (Phillips et al. 2006). For Hose's civet, we also used the jacknife validation methodology developed by Pearson et al. (2007), which has been shown to be effective for small sample sizes (25 or less).

Niche preferences/overlaps

To examine the habitat and elevation niche preferences of both species, all AC 1 and AC 2 records were plotted in ArcView and overlaid with the habitat and elevation layers. We then extracted the habitat type and elevation at each detection point, and, if available, we double-checked these with the information recorded in the field (all were congruent). Niche preferences were then defined as the frequency of occurrence within each habitat and elevation category. We used the pairwise test of Pianka (1973) to calculate the niche overlaps between these two civet species for these two variables using EcoSim 7.72 (Gotelli and Entsminger 2009). Pianka's index varies between 0 (total separation) and 1 (total overlap).

Loss of suitable habitat and level of protection

A major threat to the banded civet and Hose's civet is presumably the transformation of their preferred habitat. We assessed the loss of suitable habitat since historical times by analysing the 2010 land cover status at both historically and recently recorded localities (using a similar approach to Wilting et al. 2010). Records were defined as recent if they were collected during the last two decades (i.e., from 1992 onwards). To accommodate for the uncertainties associated with specimen locations (Graham et al. 2008), a 5-km-radius buffer zone was created around the position of all independent records (Rowe 2005). Within the buffer zones, we then compared the total percentage area of each habitat type between historical and recent records. To determine the proportion of the predicted distributions under protected areas, we first created binary maps of species presence/absence using a Maxent probability threshold value of 10 (see Pearson et al. 2007). We then overlaid these maps with the GIS layer of the World Database on Protected Areas (IUCN and UNEP-WCMC 2010) and performed calculations in ArcView to determine the percentage of each distribution that lies under protected areas.

Results

Distributions and niche preferences/ overlaps

Table 1 presents the number of records within each accuracy category, the date ranges for record groups [(AC 1 and AC 2) and (AC 3 and AC 4)] and the n values for the modelling and niche analyses. Figures 1 and 2 show the extent of occurrence and the predicted suitable areas for each species based on our Maxent modelling. The percentage occurrences of each species in each habitat category and elevation range are presented in Figures 3 and 4.

For the banded civet, the AUC value was 0.832, and the most important variable was habitat. For Hose's civet, the AUC value was 0.940, and the most important variable was elevation. The jacknife model testing for Hose's civet resulted in a high predictive success rate (86%) and highly significant models (p<0.0001).

The banded civet is found in southern Myanmar and Thailand, Peninsular Malaysia and on Sumatra, Borneo and three Mentawai Islands (Siberut, Sipora and South Pagai; Figure 1) and principally occurs in evergreen forest (99.2%; Figure 3). This species has been recorded up to 1,575 m but was mainly found at elevations below 900 m (83.2%; Figure 4). Hose's civet has only been found in evergreen forest on Borneo (Figures 2 and 3), and 66.7% of records were above 900 m (Figure 4).

The habitat niches of the banded civet and Hose's civet overlap extensively (Pianka's index=0.999), as both species primarily occur in evergreen forest (Figure 3). The



Figure 1 Predicted distribution for *Hemigalus derbyanus* within Southeast Asia based on habitat+elevation modelling. The predicted distribution is shown in grey shading, with darker colours indicating higher suitable areas. Records AC 1 and AC 2 are shown as filled-in dots ⊙, and records AC 3 and AC 4 are shown as empty dots ○.



Figure 2 Predicted distribution for *Diplogale hosei* on Borneo based on habitat+elevation modelling. The predicted distribution is shown in grey shading, with darker colours indicating higher suitable areas. Records AC 1 and AC 2 are shown as filled-in dots ③, and records AC 3 and AC 4 are shown as empty dots \bigcirc .

elevation niche overlap is lower (Pianka's index=0.359); the banded civet is principally a lowland species, whereas Hose's civet is mainly found in montane regions.

Loss of suitable habitat and level of protection

In 2010, the percentage of evergreen forest around historical banded civet records was 55.2% lower than around





recent records; for Hose's civet, the percentage of evergreen forest around historical records was 21.4% lower than around recent records (Figure 5). The proportion of predicted presence that is within protected areas is 24.1% for the banded civet and 39.4% for Hose's civet.

Discussion

Occurrence records, predicted distributions, and niche patterns

Our modelling and niche analyses have shown that the banded civet mainly occurs in lowland evergreen forest, on the Thai-Malay peninsula, Sumatra, Borneo, and three Mentawai Islands (off the western coast of Sumatra). According to our records database, the northern limit of the banded civet's distribution coincides with the Isthmus of Kra (~10° N), on the Thai-Malay peninsula. This area has traditionally been recognized as a major transition zone between the Indochinese and Sundaic zoogeographical subregions, although the range limits of many Southeast Asian mammals cluster in northern Peninsular Malaysia and where the Thai-Malay peninsula joins the main continent (Woodruff and Turner 2009). On the Mentawai Islands, specimens of the banded civet have been collected from Sipora and South Pagai Islands, and there are reports that this species is present on Siberut Island (Schreiber et al. 1989; C. Abegg, D. Boussarie, and M. Quinten personal communication). Two subspecies have been recognized on these islands (Wozencraft 2005), but this requires further investigation. The banded civet is not known to occur on any other small islands, which suggests that this species has not been transported around Southeast Asia by humans, as have some other viverrid species (Jennings and Veron 2011), or that ecological or biogeographical factors restricted their presence on other Southeast Asian islands.

The modelling and niche analyses suggested that Hose's civet occurs in evergreen forest across the higher elevation regions of Borneo. Our predicted distribution map for Hose's civet was different from those produced by Papes and Gaubert (2007): their GARP prediction showed higher probabilities of occurrence in lower elevation evergreen forest, and the Maxent model only predicted the higher elevation areas in northeast Borneo as highly suitable. These discrepancies are probably due to the differences in modelling methodologies that were used in each study: we used Maxent with accurately recorded records (mainly recent camera-trapping data) and two



Figure 4 Percentage occurrence of records AC 1 and AC 2 for *Hemigalus derbyanus* and *Diplogale hosei* at different elevations, within 300-m bandwidths.

environmental layers (habitat and elevation), whereas Papes and Gaubert (2007) used mainly museum specimen records (which can have imprecise localities) and 19 bioclimatic variables (the initial predictions were later refined using a year 2000 habitat layer).

The lowest recorded elevation for Hose's civet is at 325 meters above sea level (Samejima and Semiadi 2012; this study). There are two recent, unconfirmed reports from the lowland forests of the Lower Kinabatangan Wildlife Sanctuary (elevations below 300 m), in northeast Sabah: one possible sighting around 2005 (M. Azlan, personal communication) and another in April 2009 (Anonymous 2009; R. Munds, personal communication). Despite several enquiries, we were unable to obtain any details of the 2005 sighting, so we cannot verify or comment on this record. As for the 2009 possible sighting, the description of the animal (darkly coloured, whitish underparts, no dorsal stripes and a tail at least as long as the body) and its behaviour (feeding on fruit, high in a ficus tree) could be attributed to the small-toothed palm civet (*Arctogalidia trivrigata*), which is arboreal, can appear dark with light underparts, and dorsal stripes are not always present or visible from a distance (AJ and GV, personal observation). Moreover, a captive Hose's civet was never observed climbing in the branches within its cage (Yasuma 2004), which may indicate that this civet species is not arboreal. During 2 years of wildlife surveys in the Lower Kinabatangan area (1990–1991), Boonratana and Sharma (1997) recorded 18



Figure 5 Proportion of 2010 land cover classes within 5-km-radius buffers around historical and recent records for *Hemigalus derbyanus* and *Diplogale hosei*.

carnivore species (including five civet species), but they did not record Hose's civet. More recent survey work in this area has not reported this civet species (M. Ancrenaz, personal communication) and camera-trapping in the Lower Kinabatangan area (2010-2011) has not detected Hose's civet, even though other rare carnivore species, such as the flat-headed cat (Prionailurus planiceps), have been camera-trapped (A. Hearn and B. Goossens, personal communication). Therefore, we surmise that Hose's civet is very unlikely to occur in this lowland area of northeast Sabah. As for other outlier records, a published photograph of an animal camera-trapped in Lanjak Entimau Wildlife Sanctuary, central Sarawak, was labelled as possibly a Hose's civet (Van Rompaey and Azlan 2004). The animal's head and foreparts features are not discernable in this photograph, but the apparent lack of whitish underparts suggest that this animal was not a Hose's civet, but instead might have been a masked palm civet (Paguma larvata) or yellow-throated marten (Martes flavigula) (GV and AJ, personal observation).

Closely related, morphologically similar species commonly share ecological requirements (Anderson et al. 2002), so there is often some degree of niche differentiation to allow them to coexist (Lucherini et al. 2009, Di Bitetti et al. 2010, Jennings and Veron 2011). The niche complementarity hypothesis asserts that a high degree of overlap in one niche component should be associated with a low degree of overlap in at least one other niche dimension (Lucherini et al. 2009). Our niche analyses suggested that these two closely related civet species primarily occur in evergreen forest, yet there is a tendency for them to separate spatially along an elevation gradient: the banded civet mainly occurs in lowland areas and Hose's civet is mostly found at higher elevations. However, as there is a broad overlap of elevations at which each species can occur, and both species have been recorded at the same locations on Borneo, this elevation niche pattern does not conclusively demonstrate competitive exclusion between these two civets. In addition, the banded civet is found in Sundaic regions where Hose's civet is absent, which suggests that competitive interactions with other species might also explain its niche preferences.

Anthropogenic threats

Our study strongly indicated that the banded civet and Hose's civet are forest-dependent species that do not seem to occur in non-forested habitats. These two viverrids could, therefore, be threatened with extinction as a direct result of deforestation. Southeast Asia has the highest relative rate of deforestation of any tropical region (1%–2% per year; Sodhi et al. 2010a), and one of the main causes is the conversion of forested areas to oil palm plantations (Wilcove and Koh 2010). If present levels of deforestation continue unabated, Southeast Asia could lose up to three-quarters of its original forest cover by 2100 and 13%–85% of its biodiversity (Sodhi et al. 2010a). For both civet species, the percentage of evergreen forest in 2010 was much lower around historical records than recent records (particularly for the banded civet), which indicates that a large amount of suitable habitat has disappeared since the 1800s. Lowland forest is particularly vulnerable and disappearing fast (Meijaard and Sheil 2008), and tropical montane cloud forests are also being destroyed at alarming rates (Peh et al. 2011).

It is unknown if these two civet species are impacted by logging activities, which is a major cause of forest degradation throughout Southeast Asia (Meijaard and Sheil 2008, Sodhi et al. 2010a,b). Heydon and Bulloh (1996) found that the mean sighting frequency of banded civets (and the overall density of civet species) was significantly lower in logged forest than in primary forest. Meijaard and Sheil (2008) reviewed several studies and concluded that logging likely affects all the investigated civet species negatively. The analyses of Meijaard et al. (2008) found that a species' phylogenetic age best predicts its sensitivity to timber harvest and suggested that the banded civet is one of many species that is severely impacted by selective logging (Hose's civet was not included in this study as its phylogenetic age remains to be determined).

Habitat fragmentation has also been shown to influence the abundance, movements and persistence of many species, and forest carnivores are particularly vulnerable to local extinction in fragmented landscapes (Crooks 2002, Michalski and Peres 2005, Charles and Ang 2010). Unfortunately, we have no data for assessing the impacts and extinction risks of forest fragmentation on the banded civet and Hose's civet. For example, to determine the minimum forest patch sizes that can support viable populations, we need information on home range sizes and social organisation, which is currently lacking for these two species. Their dispersal abilities and metapopulation dynamics are also unknown. Hose's civet has a patchy predicted distribution across montane regions, and the viability of this metapopulation may be greatly affected by this species' ability to disperse through lower altitude habitats. The presence of roads throughout a forested landscape fragments major forest complexes, increases the probability of direct mortality due to vehicular traffic and allows greater human access for logging and hunting (Meijaard and Sheil 2008, Sodhi et al. 2010b), but what

impacts roads may have on civet populations is currently unknown.

Throughout Southeast Asia, viverrids are hunted for their meat to supply local and international markets and are also targeted for the wildlife trade in traditional medicines, skins, bones and pets (Corlett 2007, Shepherd 2008, Shepherd and Shepherd 2010). However, very little is known about the extent of hunting and wildlife trade of civet species or the impact that these may have on wild populations. Even if the banded civet and Hose's civet are not specifically targeted, many hunting methods, such as wire-snares, are unselective in what they catch, and non-targeted animals are often taken and killed (Corlett 2007, AJ and GV, personal observation). Clearly, increased monitoring of the wildlife trade and the level of hunting pressures are needed, as well as increased enforcement of wildlife trade and hunting regulations.

Surveying and conservation priorities

Our ENM predicted that Hose's civet has a limited distribution across the higher elevations of Borneo. As most of the records were from Brunei, Sarawak and Sabah, it is imperative that field surveys be undertaken in the montane regions of Kalimantan to determine the true extent of this species' distribution. If the range of Hose's civet is even more restricted than our prediction suggests, then this would have major implications on its conservation status; carnivore species with small geographic ranges have a high risk of extinction (Purvis et al. 2000, Cardillo et al. 2004). Similarly, we recommend that survey efforts for the banded civet are conducted in those regions where it is predicted to occur and no records currently exist. Surveys should also be conducted on Siberut Island to confirm its presence and status.

Our study has shown that 24.1% of the predicted distribution of the banded civet is currently within protected areas; the amount is higher for Hose's civet at 39.4%. This discrepancy may be explained by the large protected areas that are located in the higher elevation regions of central Borneo. We recommend that protected forests be expanded to incorporate a greater proportion of the predicted range of each species. However, as many humanrelated factors (e.g., agricultural and logging activities) would limit the expansion of protected areas, field studies are urgently needed to provide information on what would be the most effective means of increasing the level of habitat protection for these two civet species. For instance, protecting forested corridors between isolated forests could be given a high priority, yet we do not know the dispersal capabilities of these two viverrids through such habitat features, or the optimal conditions that may facilitate the movement of each species from one forest area to another.

As strictly protected areas cannot conserve the full biological diversity found within tropical forests, the fate of many species depends on what happens to forests outside protected areas. Also, forest cover is declining even within national parks and forest reserves due to illegal logging (Meijaard and Sheil 2008). Therefore, we need to gather information on the sensitivity of these two civet species to forest degradation to better understand what measures could be implemented to mitigate any detrimental impacts from logging and other destructive activities (e.g., forest fires).

Conclusion

Identifying areas of high habitat suitability for small carnivore species is very useful for planning field studies and conservation initiatives. Our study has provided a preliminary assessment of the broad-scale distribution and habitat/elevation preferences of the banded civet and Hose's civet, and shown that they are forest-dependent species that could be under considerable threats from habitat loss and other anthropogenic factors.

To test our results and to further explore the mechanisms that may be responsible for these distribution and niche patterns and the impacts of any threat, field studies are needed to gather more information on the distribution, abundance and ecology of these two civet species. Also, further work is needed to ascertain the factors determining smaller-scale habitat selection, using site occupancy models that account for imperfect detectability (Johnson et al. 2009, Kery et al. 2010, Rota et al. 2011).

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