



## Using geographic profiling to locate elusive nocturnal animals: A case study with spectral tarsiers

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**Using geographic profiling to locate elusive nocturnal animals: a case study with spectral tarsiers**

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3 1 TITLE

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5 2 **Using geographic profiling to locate elusive nocturnal animals: a case study with**  
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7 3 **spectral tarsiers**

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43 19 **Keywords**

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45 20 Geographic profiling; home range; sleep site; *Tarsius tarsier*

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- 3     26    **Short title**
- 4
- 5     27    Geographic profiling and tarsier sleeping sites
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Review Copy

28 **Abstract**

29 Estimates of biodiversity, population size, population density and habitat use have important  
30 implications for management of both species and habitats, yet are based on census data that  
31 can be extremely difficult to collect. Traditional assessment techniques are often limited by  
32 time and money, and by the difficulties of working in certain habitats, and species become  
33 more difficult to find as population size decreases. Particular difficulties arise when studying  
34 elusive species with cryptic behaviours. Here, we show how geographic profiling (GP) – a  
35 statistical tool originally developed in criminology to prioritise large lists of suspects in cases  
36 of serial crime – can be used to address these problems. We ask whether GP can be used to  
37 locate sleeping sites of spectral tarsiers (*Tarsius tarsier*) in Sulawesi, SE Asia, using as input  
38 the positions at which tarsier vocalisations were recorded in the field. This novel application  
39 of GP is potentially of value as tarsiers are cryptic and nocturnal and can easily be overlooked  
40 in habitat assessments (for example, in dense rainforest). Our results show that GP provides a  
41 useful tool for locating sleeping sites of this species, and indeed analysis of a preliminary data  
42 set during field work strongly suggested the presence of a sleeping tree at a previously  
43 unknown location; two sleeping trees were subsequently found within five metres of the  
44 predicted site. We believe that GP can be successfully applied to locating the nests, dens or  
45 roosts of elusive animals such as tarsiers, potentially improving estimates of population size,  
46 with important implications for management of both species and habitats.

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3 47 **Introduction**  
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5 48 The ability to accurately and reliably detect and locate individuals is vital for assessing  
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7 49 animal population density and dynamics, habitat use and ranging patterns – crucial  
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10 50 information that underpins the development of conservation management plans for both  
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12 51 species and their habitat (Tyre *et al.*, 2003). Traditional census and survey techniques are  
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14 52 often limited by time constraints, prohibitive costs and the challenging logistics of certain  
15  
16 53 habitats. Particular difficulties arise when studying elusive species with cryptic behaviours  
17  
18 54 (MacKenzie *et al.*, 2005; Neilson *et al.*, 2013), or species with declining populations, since  
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20 55 animals become more difficult to find as population size decreases (Neilson *et al.*, 2013;  
21  
22 56 Chades *et al.*, 2008).  
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28 58 Researchers attempting to census such species typically encounter two main problems. First,  
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30 59 the overall study area is often too large to explore exhaustively and inferences must therefore  
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32 60 be made using a smaller sampling location, for example using a probabilistic sampling  
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34 61 method (MacKenzie *et al.*, 2005). Second, variation arises due to detectability, and research  
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36 62 must take into account the likelihood that many individuals will go undetected even though  
37  
38 63 they may be present (Neilson *et al.*, 2013; Chades *et al.*, 2008). In this study, we ask whether  
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40 64 geographic profiling, a statistical method commonly used in criminology (Rossmo, 2000) and  
41  
42 65 increasingly being applied to biological data (Le Comber *et al.*, 2006; Martin *et al.*, 2009;  
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44 66 Raine, Rossmo & Le Comber, 2009; Le Comber *et al.*, 2011; Le Comber & Stevenson, 2012;  
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46 67 Stevenson *et al.*, 2012; Papini *et al.*, 2013; Verity *et al.*, 2014), can be used to improve  
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48 68 surveys of species that are rare and/or elusive.  
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54 70 In criminology, geographic profiling uses the spatial locations of a series of linked crimes to  
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56 71 calculate the probability of offender residence for each location within the study area,  
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3 72 producing a three-dimensional probability surface called a jeopardy surface; overlaid on a  
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5 73 map of the study area, this is termed a geoprofile. Suspect sites are prioritised according to  
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7 74 their height on the geoprofile (Rossmo, 2000). Geographic profiling was designed to solve  
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10 75 the problem of information overload when dealing with cases of serial crime, since such  
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12 76 cases typically generate too many suspects rather than too few, and resources will often  
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14 77 preclude a detailed investigation of them all: for example, police investigating the case of the  
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16 78 Yorkshire Ripper accrued 268,000 suspect names and 5.4 million vehicle registration  
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18 79 numbers (Doney, 1990; Rossmo, 2000). Similar constraints – lack of time, lack of resources –  
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21 80 will obviously also often apply in conservation.  
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25 82 Geographic profiling has been extremely successful in criminology, and is routinely used by  
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27 83 organisations including the Royal Canadian Mounted Police, the Bureau of Alcohol,  
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29 84 Tobacco, Firearms and Explosives, the Los Angeles Police Department, the National Crime  
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31 85 Agency in the UK and the United States Marine Corps (Rossmo, 2012). This success has led  
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33 86 to its application to biological data, notably animal foraging (where it can be used to find  
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35 87 animal nests or roosts using the locations of foraging sites as input) (Le Comber *et al.*, 2006;  
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37 88 Martin *et al.*, 2009; Raine *et al.*, 2009; Le Comber & Stevenson, 2012), epidemiology  
38  
39 89 (identifying disease sources from the addresses of infected individuals) (Le Comber *et al.*,  
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41 90 2011; Le Comber & Stevenson, 2012; Verity *et al.*, 2014) and invasive species biology (using  
42  
43 91 current locations to identify source populations) (Le Comber & Stevenson, 2012; Stevenson  
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45 92 *et al.*, 2012) (Table 1). More recently, a version of the model based on a Dirichlet Process  
46  
47 93 Mixture (DPM) model that outperforms the Criminal Geographic Targeting (CGT) algorithm  
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49 94 used in criminology has been developed and applied to biological data (Verity *et al.*, 2014).  
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3 96 Here, we apply this model to a small, cryptic nocturnal primate species, the spectral tarsier  
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5 97 *Tarsius tarsier*. There are 10 extant species of tarsier, and eight of these are endemic to the  
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7 98 Indonesian island of island of Sulawesi (Shekelle *et al.*, 2008; Merker *et al.*, 2009); however,  
8  
9 99 there may well be many more species that have yet to be described (Shekelle, 2010). Tarsiers  
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11 are nocturnal, roosting in trees and crevices during the day, but sleeping sites vary depending  
12  
13 100 on forest type. In most cases tarsiers will be found sleeping in the crevices of strangler figs.  
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15 101 They are the only extant obligatory carnivorous primates, feeding exclusively on live  
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17 102 animals, predominantly insects. Their small size (100-150g), nocturnal lifestyle and ability to  
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19 103 leap, almost silently, between branches in the forest make them difficult to locate in the field  
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21 104 (MacKinnon & MacKinnon, 1980). Understanding tarsier population dynamics and home  
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23 105 ranges is critical to understanding their likely response to habitat change and destruction.  
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25 106 However, many tarsier species are either critically endangered or listed by the International  
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27 107 Union for Conservation of Nature (IUCN, 2013) as data deficient, meaning that there are  
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29 108 insufficient data for a proper IUCN assessment. Many tarsier species have been extensively  
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31 109 studied, but much of this relates to aspects of their biology such as their phylogeny (for  
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33 110 example, Merker *et al.*, 2014 and Pozzi *et al.*, 2014), and there is less information on their  
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35 111 distribution or population size (IUCN, 2013).  
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41 114 Lowland forest is thought to contain the highest diversity and abundance of animal and plant  
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43 115 species and, with the exceptionally high biodiversity in SE Asian forests, in conjunction with  
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45 116 carbon storage within the peatlands, deforestation of this area is of global concern. Despite  
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47 117 this, deforestation is occurring at a rapid rate within Indonesia itself (Whitten, 2000; Whitten,  
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49 118 Mustafa & Henderson, 2002; Miettinen *et al.*, 2011a). Globally, Indonesia has exhibited the  
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51 119 largest increase in forest loss between 2000 and 2012, with a low of 10,000km<sup>2</sup> lost per year  
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53 120 to a high of over 20,000km<sup>2</sup>. Further analyses of spatial resolution land maps have revealed  
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3 121 an overall yearly decline of 1% of forest cover, with the main destruction occurring within  
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5 122 plantations and secondary vegetation. (Hansen *et al.*, 2013; Miettinen *et al.*, 2011a,b). These  
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7 123 recent studies show that deforestation is still occurring at a high rate in SE Asia, endangering  
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9 124 many endemic forest species, such as the tarsier, and habitat destruction leading to the loss of  
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11 125 suitable habitat has led to the IUCN classifying two species of tarsier, the spectral tarsier  
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13 126 *Tarsius tarsier* and Dian's tarsier *T. dentatus*, as vulnerable. This vulnerable status is  
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15 127 primarily driven by habitat loss rather than population number (Shekelle, Merker & Salim,  
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17 128 2008; Shekelle *et al.*, 2008).  
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23 130 One way to estimate tarsier numbers is via identification of their roost sites (Fig. 1a). In  
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25 131 practice, though, this is extremely difficult, and is usually carried out by tracking the animals  
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27 132 using their duet vocalisations – characteristic calls made prior to dawn each morning as pairs  
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29 133 return to their sleeping sites (MacKinnon & MacKinnon, 1980). However, the short overall  
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31 134 duration of the duetting period, and rapid sound attenuation in the dense rainforest typical of  
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33 135 this species' habitat, mean that actually locating individuals from their duets is at best  
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35 136 difficult and time consuming, and at worst impossible. Other methods of estimating  
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37 137 population numbers, such as camera trapping, are arguably less labour intensive but perhaps  
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39 138 less effective (Foster & Harmsen, 2012) and in any case also present logistical difficulties  
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41 139 due to the dense habitat (Fig. 1b); camera trapping is also expensive.  
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47 141 Here, we use the DPM implementation of the geographic profiling model (Verity *et al.*, 2014)  
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49 142 to identify likely sleeping sites, with locations of duet vocalisations representing 'crime sites'  
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51 143 and the sleeping sites analogous to an offender's 'anchor point'. To test this model, we take a  
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53 144 retrospective approach, using data on vocalisations and sleeping trees that were collected in a  
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55 145 previous study. We suggest that this approach has the potential to provide a more efficient  
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3 146 way to identify physical locations of elusive, cryptic species such as the spectral tarsier, and  
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5 147 to improve estimates of population size, population density and home range size for such  
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7 148 species.  
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## 12 151 **Methods**

### 13 152 Study area

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18 153 This project was conducted on Buton Island, Southeast Sulawesi, Indonesia (longitude  
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20 154 123°12' E-122° 33'E and latitude 5°44' S-4° 21' S; Fig. 2). Buton has a length of 100 km and  
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22 is 42 km at its widest point, and an area of approx. 4,520 km<sup>2</sup> (Priston *et al.*, 2011). The  
23 155 forest where sampling took place is split into two reserves, separated only by a small road:  
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25 156 Kakanauwe Nature Reserve (810 ha) and Lambusango Wildlife reserve (28,500 ha) (Martin  
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27 157 & Blackburn, 2010). Buton Island experiences a tropical climate, with a pronounced dry  
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29 158 season between August and October, and a wet season between October and April; there is  
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31 159 variable rainfall between May and July each year (Whitten 2000; Whitten *et al.*, 2002;  
32  
33 160 Gillespie *et al.*, 2004). The traditional economy is based on subsistence farming, arising from  
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35 161 slash and burn agriculture (Priston *et al.*, 2011). The main anthropogenic impacts on the  
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37 162 Buton rainforest are forest clearance for land use such as subsistence farming, illegal logging,  
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39 163 asphalt mining and rattan collection (Priston *et al.*, 2001).  
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### 48 166 Field data collection

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50 167 Research was undertaken between May and August 2013. Surveys started before 05:00 each  
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52 168 morning, and continued until approximately 06:00. Before dawn, between 05:00 and 06:15,  
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54 169 mated pairs of tarsiers make shrill, sexually dimorphic vocalisations that last up to four  
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56 170 minutes as they are returning to roost; these are repeated as the animals move closer to the  
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3 171 sleeping sites, covering in total a period of around 20 minutes (Faulkner, pers. obs.). Each  
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5 172 morning, after the first tarsier was heard, the observer remained static and noted the time of  
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7 173 day. GPS data on the location of the observer were recorded, and distance/compass bearing of  
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10 174 the vocalising animals from the observer estimated. The observer then attempted to follow  
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12 175 the tarsiers to the sleeping tree; where this was possible, its precise location was recorded. A  
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14 176 sleeping site was only classed as such if a tarsier or tarsiers were seen entering a tree, vine  
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16 177 tangle or rock crevice. A total of 25 sleeping trees were identified during the study, including  
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18 178 two located using output from a preliminary GP analysis carried out during data collection;  
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20 179 since these were not independent of the model they were excluded from the final analysis.  
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### 25 181 Geographic profiling

27 182 The DPM model of geographic profiling, which is fully described in Verity *et al.* (2014),  
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29 183 provides a mathematically robust method of estimating source locations from the spatial  
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31 184 locations of the observed crime sites. Conceptually the method can be split into two parts.  
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33 185 First, the crime sites are partitioned into distinct clusters, with crimes that are close to one  
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35 186 another being more likely to end up in the same cluster. It is assumed that all points within a  
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37 187 cluster originated from the same source, while points in different clusters originated from  
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39 188 different sources. Second, conditional on a particular partition of the data into clusters, the  
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41 189 posterior distribution of the unknown source locations is calculated using a method analogous  
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43 190 to that described by O'Leary (2010). By alternating between these two steps using standard  
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45 191 Markov Chain Monte Carlo (MCMC) methods it is possible to reconstruct the full posterior  
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47 192 distribution of the source locations, integrated over all possible partitions of the data into  
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49 193 groups.  
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3 195 In our case we were interested in using the spatial locations of tarsier vocalisations as input to  
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5 196 the DPM model, and using the resulting geoprofile to construct a prioritised search strategy  
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7 197 when looking for sleep sites. By carrying out this analysis retrospectively, on data in which  
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9 198 the true sleep sites (or at least a subset of the true sleep sites) are known, we can measure the  
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11 199 effectiveness of this search strategy compared with a number of alternative approaches.  
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16 201 Finally, we note that although the terminology used in geographic profiling (crime sites,  
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18 202 offender residence, etc.) is not always appropriate for use with biological data, for  
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20 203 consistency with the criminological literature we will here refer to tarsier sleeping tree sites  
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22 204 as anchor points or source locations and vocalisation location sites as crime sites.  
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#### 26 27 206 Model implementation

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29 207 The DPM model was implemented in R (R Core Team, 2012) using the package Rgeoprofile  
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31 208 as described by Verity *et al.* (2014); this package is available from  
32  
33 209 <http://evolve.sbcs.qmul.ac.uk/lecomber>, or from the authors on request. Model parameters  
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35 210 were set to default values, with the exception of sigma, the distance (in lat/long degrees)  
36  
37 211 representing one standard deviation of the bivariate normal distribution centred on the source.  
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39 212 This was set to 0.0009, corresponding to a distance of 100m at the study site location. This is  
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41 213 equivalent to stating that 99% of the ‘crime sites’ are expected to occur within a circle of  
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43 214 radius 300m centred on the source. This is consistent with the (admittedly sparse) literature  
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45 215 on the dispersal distances of tarsiers, which report them as having nightly path lengths of  
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47 216 roughly 1 km (Merker, 2006; Neri-Arboleda *et al.*, 2002).  
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#### 52 53 218 Model evaluation

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3 219 Model output can be assessed using the hit score, the proportion of the area covering the  
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5 220 crimes (in this case, the positions at which tarsiers were recorded, plus a ‘guard rail’ of 5 %  
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7 221 surrounding this) in which the anchor point/s (sleep tree/s) are located. The hit score is  
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10 222 calculated by dividing the ranked score by the total search area. The smaller the hit score, the  
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12 223 more efficient the search strategy described by the model; a hit score of 0.5 (50%) is what  
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14 224 would be expected from a nonprioritised (i.e. random or uniform) search (Rossmo, 2000).  
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## 227 **Results**

### 228 Field study

229 In total, 190 tarsier call locations were recorded across 45 mornings of sampling, within both  
230 the Kakanauwe and Lambusango forest reserves. A total of 15% of the vocalisations were  
231 recorded between 05:00 and 05:30, 47% between 05:30 and 05:45, 34% between 05:45 and  
232 06:00 and 4% after 06:00). This follows previously published data on the timing of tarsier  
233 calls (Neitsch 1999; MacKinnon & Mackinnon 1980). We identified 25 sleeping sites, mostly  
234 large strangler fig trees (Fig. 1a), but dense vine tangles and dead tree trunks were also used.  
235

### 236 Preliminary analysis

237 Although the analysis here is retrospective, we ran the model on an early partial data set  
238 while field work was still in progress. This preliminary analysis strongly suggested the  
239 presence of a sleeping tree in the NW part of the study area; two sleeping trees were  
240 subsequently found within 5 m of the predicted location (Fig. 3). Since these two sleeping  
241 trees were not independent of the model, they were not used to test the model and were  
242 excluded from the full analysis reported below.  
243

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3 244 Full analysis  
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5 245 The mean hit score for the 23 sleeping trees identified during field work (excluding an  
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7 246 additional two sleeping trees identified in the preliminary analysis) was 0.16 (sd = 0.154); the  
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9 247 median hit score was 0.15. The model found 10 of the sleeping trees after searching less than  
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11 248 10% of the total map area of 3.4 km<sup>2</sup>, and 16 after searching less than 20% (Fig. 4, Fig. 5).  
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17 251 **Discussion**  
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20 252 These results show that the DPM model of geographic profiling described in Verity *et al.*  
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22 253 (2014) can successfully be used to prioritise the search for tarsier sleeping sites. We suggest  
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24 254 that the DPM model could be used to help locate nests, dens or roosts of other rare and hard-  
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26 255 to-study animals, potentially improving estimates of population size in these cases, and  
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28 256 allowing important management decisions at both the species and habitat level to be based  
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30 257 on better data. In fact, although the analysis here is retrospective, the DPM model of  
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32 258 geographic profiling also proved useful in practice, with a preliminary analysis successfully  
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34 259 predicting the locations of two sleep trees that were subsequently confirmed in the field.  
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36 260 While we would be cautious about inferring too much from such a limited example, we note  
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38 261 that this is the first time that GP has been used in biology as a prelude to further investigation  
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40 262 and at the very least demonstrates the potential of this approach.  
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47 264 The ability to locate tarsier roost sites quickly and efficiently is of critical importance if  
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49 265 conservation strategies are to be put into place to help conserve this species. Although there is  
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51 266 limited destruction occurring on Buton itself in comparison to other areas, and although many  
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53 267 tarsier species, including the spectral tarsier, often do prefer secondary forest, possibly due to  
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55 268 increased insect abundance arising as a consequence of disturbance, as has been suggested in  
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3 269 other contexts (Zhang *et al.*, 2014) and locomotory aids from smaller trees (Merker *et al.*,  
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5 270 2005), there will be a limit to how much disturbance this species can tolerate before  
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7 271 population numbers begin to decline. The use of GP to better target behavioural studies and  
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9 272 gain more accurate information on the species' ecology could thus be of considerable  
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11 273 practical use.  
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16 275 Large cavity-bearing trees provide important ecological functions such as nesting and  
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18 276 denning resources for many species (Lindenmayer *et al.*, 2012). The overall decline in cavity-  
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20 277 bearing trees such as the strangler fig is an emerging conservation concern, due to the  
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22 278 importance of these trees to a variety of cavity-dwelling wildlife including tarsiers, other  
23  
24 279 mammals, birds and invertebrates (Struebig *et al.*, 2013). Forests are not recruiting these  
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26 280 trees fast enough due to the extended period required for their replacement once they are  
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28 281 destroyed (Lindenmayer *et al.*, 2012). A study by Cockle *et al.* (2010) showed that logging  
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30 282 was reducing the basal area of primary forests by half and therefore reducing the number of  
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32 283 trees with suitable cavities for nesting animals. However, there are limited studies on the  
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34 284 availability of these cavity-bearing trees in Southeast Asian rainforests (Cockle *et al.*, 2010;  
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36 285 Struebig *et al.*, 2013).  
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43 287 There are numerous advantages to using GP rather than other more simple measures of  
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45 288 spatial tendency such as spatial mean, spatial median and centre of minimum distance. Chief  
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47 289 among these is the fact that the DPM model can deal with multiple sources (eg, multiple roost  
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49 290 sites in this study), as opposed to providing a single point estimate for a single source or roost  
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51 291 site. In criminology, Rossmo & Velarde (2008) made direct comparisons between measures  
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53 292 of spatial tendencies and the CGT (Criminal Geographic Targeting) algorithm used in  
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55 293 geographic profiling and showed that GP is three times more effective at detecting the anchor  
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3 294 points of serial offenders, while in ecology, in a study looking at source populations of  
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5 295 invasive species, Stevenson *et al.* (2012) found that the CGT algorithm outperformed other  
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7 296 measures of spatial central tendency (spatial mean, spatial median, centre of minimum  
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9 297 distance and a kernel density model) in 52 of the 53 species studied.  
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14 299 Although the results from this study are highly promising, geographic profiling is still in the  
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16 300 initial stages of application to the field of biology. For example, not all species will offer a  
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18 301 conspicuous vocalisation like the elusive tarsier; however, other measurable parameters  
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20 302 abound. These include sightings, scat evidence or GPS data from radio collars, for example,  
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22 303 all of which could potentially be used as ‘crime sites’ to help locate the animals’ anchor  
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24 304 points (nests, dens or roosts). However, it is striking how well even this simple model  
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26 305 performs: using other dispersal distributions (eg Cauchy distributions) or incorporating more  
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28 306 complex priors based on habitat information could all add power to the model.  
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34 308 In conclusion, this study suggests that GP could be useful when searching for elusive and rare  
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36 309 species such as tarsiers, increasing search efficiency, improving estimates of population  
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38 310 numbers and range size and leading to more efficient use of scarce resources such as time,  
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40 311 money and personnel.  
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Review Copy

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7 420 **Figure 1** (a) A sleeping tree; (b) Typical habitat within the study site.  
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11 422 **Figure 2** Buton Island. The area in the red square represents the two forested reserves  
12 (Kakanauwe and Lambusango) where the study took place.  
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17 425 **Figure 3** Geopofile showing the results of the preliminary analysis. Red circles show the  
18 426 positions of the observer when tarsier vocalisations were recorded, and blue squares the two  
19 427 sleeping trees whose locations were successfully predicted in this analysis. Contours show  
20 428 bands of 5%, with lighter colours corresponding to higher parts of the geopofile.  
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24 430 **Figure 4** (a) Geopofile showing the results of the final analysis. As before, red circles show  
25 431 the positions of the observer when tarsier vocalisations were recorded, and blue squares the  
26 432 sleeping trees. Contours show 5% increments. (b) The raw probability scores (p) underlying  
27 433 the geopofile in (a).  
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31 435 **Figure 5** Histogram showing the hit scores for all 23 sleeping trees in the final analysis.  
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437 **Table 1** Geographic profiling's application in criminology, biology and epidemiology

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Field	Crime sites	Suspect sites	References
<i>Criminology</i>			
Murder, rape, burglary, arson	Spatial locations of linked crime sites (eg murders)	Areas likely to be associated with the offender (eg a home or workplace)	Rossmo 2000 and many others
<i>Biology</i>			
Animal foraging	Spatial locations of foraging sites	Possible nests, roosts, dens etc	Le Comber <i>et al.</i> , 2006; Martin <i>et al.</i> , 2009; Raine <i>et al.</i> , 2009
Invasion biology	Spatial locations of current populations of invasive species	Areas associated with source populations	Stevenson <i>et al.</i> , 2012; Papini <i>et al.</i> , 2013
<i>Epidemiology</i>			
Malaria, cholera	Spatial locations of infected individuals	Vector breeding sites or other sources of infection (eg contaminated water)	Buscema <i>et al.</i> , 2009; Le Comber <i>et al.</i> , 2011; Verity <i>et al.</i> , 2014

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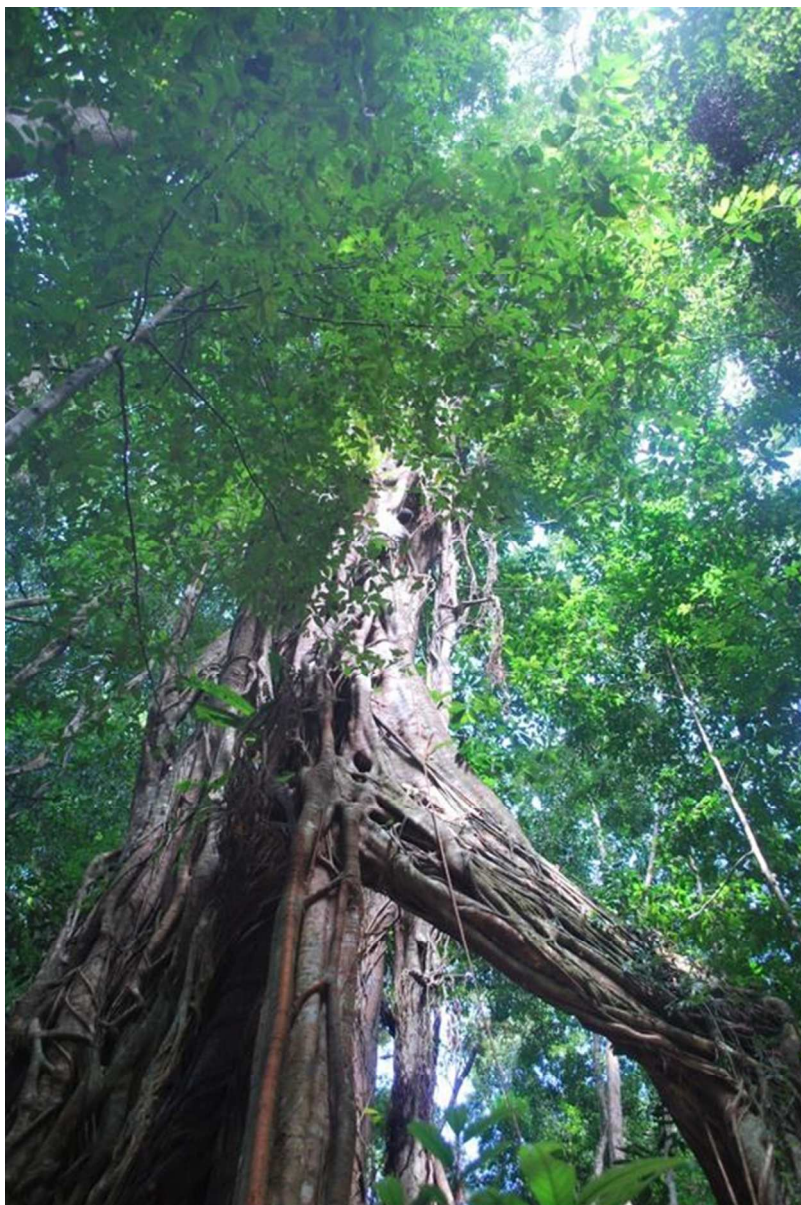


Figure 1 (a) A sleeping tree; (b) Typical habitat within the study site.  
189x282mm (72 x 72 DPI)



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Figure 1 (a) A sleeping tree; (b) Typical habitat within the study site.  
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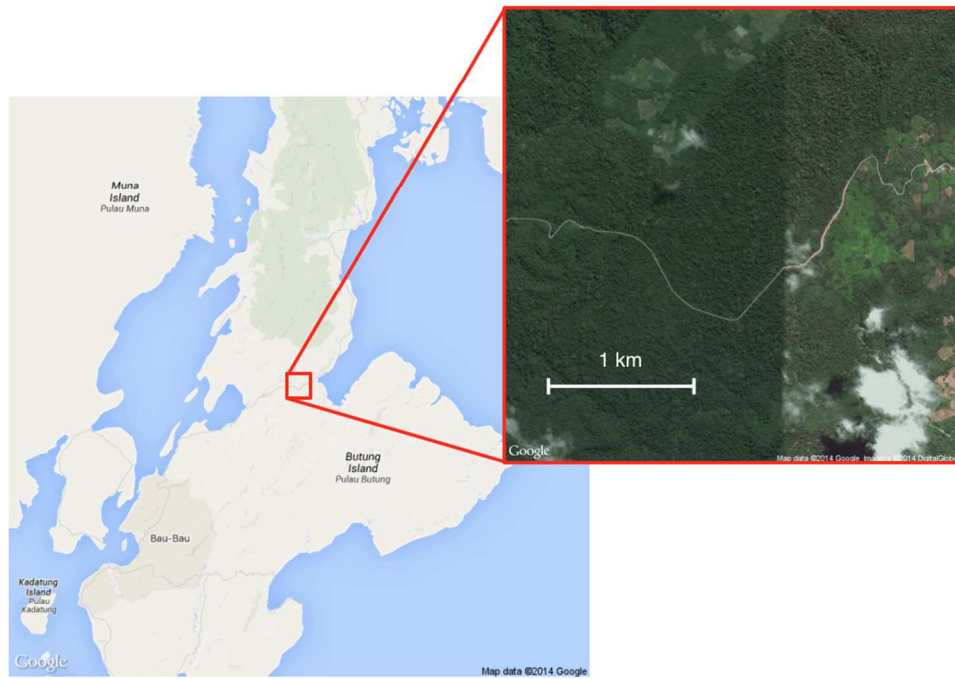


Figure 2 Buton Island. The highlighted area represents the two forested reserves (Kakanauwe and Lambusango) where the study took place.  
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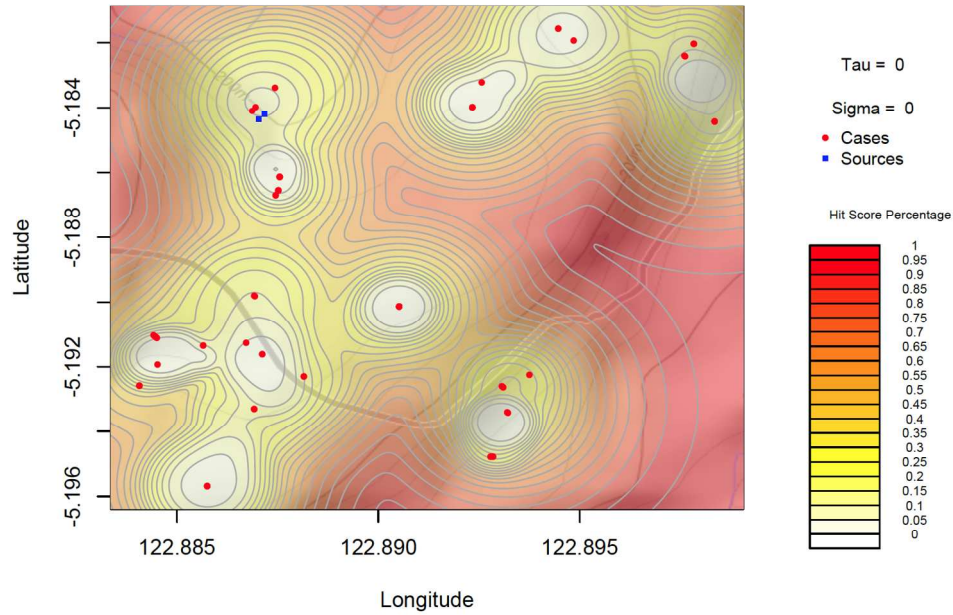


Figure 3 Geoprofile showing the results of the preliminary analysis. Red circles show the positions of the observer when tarsier vocalisations were recorded, and blue squares the two sleeping trees whose locations were successfully predicted in this analysis. Contours show bands of 5%, with lighter colours corresponding to higher parts of the geoprofile.  
614x451mm (72 x 72 DPI)

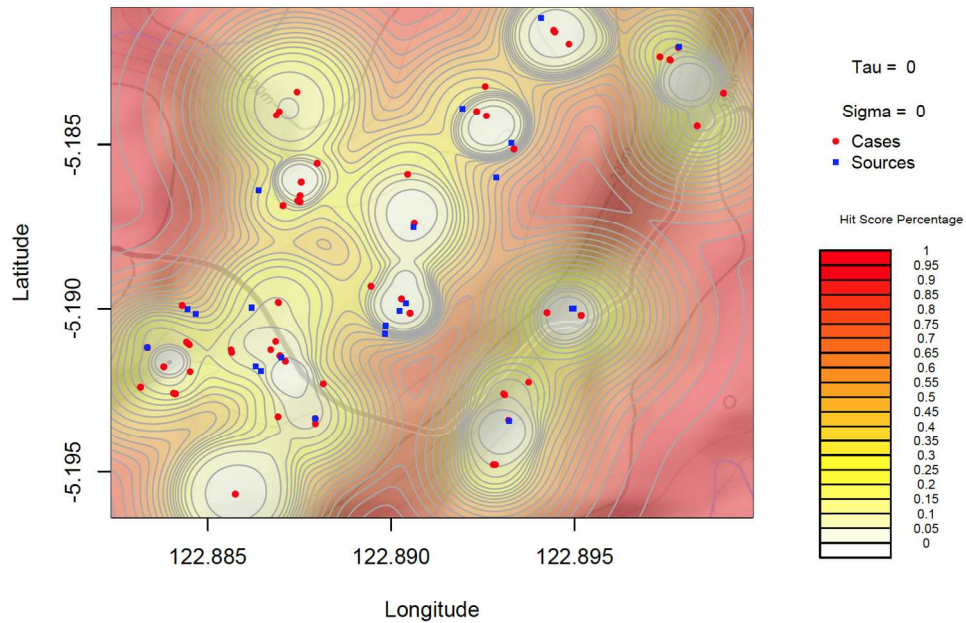


Figure 4 (a) Geoprofile showing the results of the final analysis. As before, red circles show the positions of the observer when tarsier vocalisations were recorded, and blue squares the sleeping trees. Contours show 5% increments. (b) The raw probability scores underlying the geoprofile in (a).  
606x452mm (72 x 72 DPI)

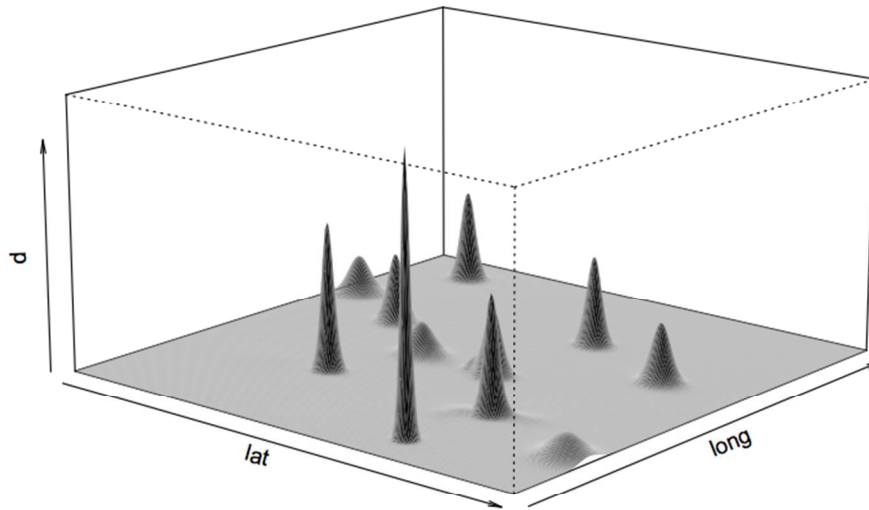


Figure 4 (a) Geoprofile showing the results of the final analysis. As before, red circles show the positions of the observer when tarsier vocalisations were recorded, and blue squares the sleeping trees. Contours show 5% increments. (b) The raw probability scores underlying the geoprofile in (a).  
287x196mm (72 x 72 DPI)

