THE RAFFLES BULLETIN OF ZOOLOGY 2010 **58**(1): 157–164
Date of Publication: 28 Feb.2010

POPULATION ASSESSMENT METHODS FOR THE SUNDA COLUGO *GALEOPTERUS VARIEGATUS* (MAMMALIA: DERMOPTERA) IN TROPICAL FORESTS AND THEIR VIABILITY IN SINGAPORE

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ABSTRACT. – Colugos are arboreal folivores and are found in tropical rainforests of Southeast Asia. Despite their discovery roughly 200 years ago, colugos attracted relatively little scientific attention. Given the importance of population estimates in conservation decision-making, it is surprising that no colugo has been surveyed in tropical forest habitats. In this study, we assessed the possibility of using distance-sampling for estimating population size of Sunda Colugo (*Galeopterus variegatus*) in the protected forests of Singapore, and also compared this method with estimates from fixed-width strip transect. We found that key assumptions of distance-sampling were not violated and the method provided relatively more precise estimates than fixed-width strip transect. The population density estimate obtained was 0.535 (± 0.104) individuals per ha, and this translates to an estimated 1,074 ± 209 individuals within the 2,007 ha of protected forests in Singapore. We recommend the use of distance-sampling for the long-term monitoring of colugo populations and also discuss the viability of the species in Singapore.

KEY WORDS. – Flying lemur, distance-sampling, population estimate, fixed-width transect, conservation.

INTRODUCTION

The mammal order Dermoptera comprises two species of colugos (or flying lemurs). These include the Sunda Colugo (*Galeopterus variegatus*) which resides in Java, Sumatra, Borneo, Malay Peninsula, Southeast Asian mainland (Medway, 1978; but see Janečka et al., 2008) and recently documented from northern Laos (Ruggeri et al., 1998), and the Philippine Colugo (*Cynocephalus volans*; known locally as kagwang) which occurs only in the southern islands of the Philippines (Mendoza et al., 2001). Colugos are arboreal folivores and are found in tropical rainforests (Lim, 2007). Their most striking feature is the extensive gliding membrane (or patagium) which enables them to travel up to 136 m in a single glide, and a corresponding decline in vertical height of 10.5 to 12 m (Walker, 1983).

However, perhaps because of their nocturnal habits, cryptic coloration and that they seldom vocalise, colugos attracted relatively little scientific attention. Despite their discovery roughly 200 years ago, much of the available literature on their life history and behaviour has been based on sporadic field observations, and are mostly anecdotal (e.g. Medway, 1978, Lekagul et al., 1988, Mendoza et al., 2001). Only a handful of studies have focused on the behaviour and ecology of colugos. The first was an unpublished Honours year thesis (Tan, 1972), which reported on the behaviour of Malaysian *G. variegatus* in captivity. Unfortunately, this was never published and remains unavailable to most workers. The other was a Ph.D. dissertation on *C. volans* (see Wischusen 1990; Wischusen et al., 1989, 1992, 1998) which investigated various aspects of foraging behaviour and social behaviour. The final study was a report on population size and diet of *G. variegatus* in a managed landscape of ca. 68 ha in Singapore (Agoramoorthy et al., 2005). These studies yielded some results contrary to information mentioned in older literature. For instance, most older records suggest a gestation period of 60 days but failed to present methods employed or concrete evidence (see Kenneth et al., 1953); a much longer duration (150 days) was suggested by Wischusen et al. (1992) for *C. volans* and even longer (180 days) by Tan (1972) for *G. variegatus*.

Surprisingly, no colugo has been rigorously surveyed in their natural habitat of tropical forests. Even the study by Agoramoorthy et al. (2005) was undertaken in a largely landscaped environment at the Singapore Zoo. Many biological studies require estimates (or absolute number) of population size or rate of population change, and land-use managers require such baseline data to understand specific habitat requirements, to justify conservation actions, and to assess the success or failure of any such actions. Various census techniques exist (e.g. total counts, mark-recapture methods, point and line transects; Sutherland, 1996) and the technique should be selected based on the habitat, resource limitations and the species of interest. Even with the multitude of census techniques for different species, most are mathematical models and thus require assumptions which may be difficult or impossible to fulfill in the field (Seber, 1982). In addition, the extent to which individuals vocalise, variation in the likelihood of being seen or caught, and their movement patterns all influence the accuracy of census techniques (Greenwood, 1996). Therefore, it is important for workers to be aware of these limitations and plan their methodology carefully. Census of arboreal species is especially difficult and can often yield highly variable data (e.g. Carlos, 1996, Lindenmayer et al., 2003). This is especially true for cryptic and nocturnal arboreal species, and is perhaps a key reason behind the lack of ecological studies on colugos.

Wischusen (1990) suggested that the highest priority for further research on colugos is to estimate population sizes of these species, but he also recognised the difficulties of conducting census in the tropical rainforest habitat. Perhaps due to the cryptic and inconspicuous nature of colugos, they were often perceived to be rare and/or endangered. For example, Ho et al. (1994) gave a conservative estimate of 200 individuals in Singapore based on what their group observed, and as such, the species was regarded as highly endangered. Nevertheless, based on personal sightings of the flying lemurs over the past years and recorded sightings in various places of Singapore (e.g. Yeo, 1991, Yeo et al., 1992, Subaraj et al., 1995), the population of Singapore colugos almost certainly exceeds the conservative estimate of Ho et al. (1994), and in the latest assessment of Singapore mammal fauna, the species has been removed from the threatened list (see Davison et al., 2008).

Censuses typically employ fixed-width strip transects, which assume that all subjects within the strip transect are detected (Greenwood, 1996). Unfortunately, this method has limited applications for arboreal cryptic species in complex environment like closed forest, because the probability of detecting the subject falls rapidly with increasing distance from the observer. Distance-sampling (also known as variable-width transect), on the other hand, models the detection function based on the decline in observations with increasing distance (x) and requires only that all objects on the transect line are detected (i.e. $x = 0$; Buckland et al., 1993). Additionally, distance-sampling requires objects to be detected at their initial location and assumes that distances are measured accurately (Buckland et al., 1993).

We assessed the possibility of using distance-sampling (Burnham et al., 1985, Buckland et al., 1993) for estimating population size of the Sunda Colugo (*G. variegatus peninsulae*) in the tropical forests in Singapore, and also compare this method with estimates from fixed-width strip transect. We provide an estimate for the population density in Singapore and also discuss the viability of the species in Singapore.

METHODS AND MATERIALS

Study Site. **–** We studied colugos in mainland Singapore (1°16'N 103°51'E), an island state 699 km^2 in area and situated at the southern tip of the Malay Peninsula. The climate is characterised by high relative humidity, temperature (daily mean: 84.3% and 26.8°C respectively) and rainfall (annual rainfall approximately 2,344 mm) (Tan et al., 2007).

The primeval vegetation of Singapore was primarily lowland evergreen rainforest, which occupied about 82% of the area in the 1800s (Chou et al., 2006). Urbanisation and population growth (currently about 4 million), these forest have been reduced to just 279 ha, with a further 1,560 ha covered in tall secondary forest (Corlett, 1997, Tan et al., 2007). The Central Catchment Nature Reserve possesses the largest continuous tracts of old secondary forest in Singapore; this vegetation can be distinguished from primary forests by a lower canopy and the absence of emergent species such as the dipterocarps (Chou et al., 2006). The prominent species in such forests include *Rhodamina cinerea*, *Calophyllum* species, *Macaranga* species and *Archidendron clyperia* (see Tan et al., 2007). The Central Catchment Nature Reserve also includes 168 ha of young regenerating forests that typically have lower and incomplete canopy cover.

Transect survey. **–** We conducted 61 variable-width transects (each 200 m long) within the protected forests of Bukit Timah Nature Reserve and Central Catchment Nature Reserve. To reduce the influence of edge effects, we restricted the censuses to small footpaths or trails (< 2 m wide) which were under continuous canopy cover of the rain forest. To minimise stochastic influences, we surveyed each transect three times throughout the sampling period of February to June 2006.

We only recorded sightings by the first author; this eliminated observer differences (e.g. height differences and search image of the observer) which can lead to problematic estimates (Buckland et al., 1993). We walked each transect between 2000 and 2359 hours, on nights without strong winds or rain. This is known to be the active period of the Philippine Colugo (Wischusen & Richmond, 1998), and the authors have also observed most activity during this period for *G. variegatus*. Surveys were conducted at a speed of about 1 km h^{-1}, similar to velocities reported in other closed terrain transects (e.g. Carlos, 1997, Chiarello et al., 2001). We employed small spotlights (3-watt L.E.D. flashlights) whenever visibility allowed. Scanning at further distances and confirmation of sightings was done with a 1,000,000 candlepower spotlight and Leitz 10 × 40 BA Trinovid binoculars. Extra care and effort was concentrated on the scanning of trees near the transect line. This was because the most important assumption for distance-sampling is that all animals on the line must be detected (Buckland et al., 1993).

We recorded the perpendicular distance of the animal from the centre of the footpath using a measuring tape (< 14 m) or laser rangefinder (> 14 m; Bushnell Yardage Pro, Bushnell Corporation, USA). Only independent colugos were recorded for calculation of population density (i.e. we excluded dependent young clinging to their mothers). Any unweaned young normally are hidden within the patagium, rendering it almost impossible to ascertain their presence on every occasion. Additionally, independent animals are of greater ecological significance since they are the essential consumers of resources.

Distance-sampling analysis. – We pooled all sightings and analysed them using software DISTANCE (version 5.0; Buckland et al., 1993). Before model fitting, we truncated the furthest 5% of observations because they are difficult to model and provided little information for estimating the density function at zero distance, the most crucial part of the curve. In addition, truncation often reduces bias and/or improves precision in density estimates (Buckland et al., 1993). In the exploratory phase, the following five models were utilised to generate the density estimate: a uniform key function adjusted with either a cosine series expansion or simple polynomial series expansion, a half-normal key function adjusted with cosine series expansion or Hermite polynomials, and a hazard-rate key function adjusted with cosine series expansion.

The criterion for selecting the best-fit model was minimum Akaike's Information Criterion (AIC); AIC provides a quantitative method of model selection (Akaike, 1985) and is an integral part of DISTANCE software (Buckland et al., 1993). The best-fit model was also checked for fit near zero distance in the detection histogram (to investigate whether the most important assumption, full detection on the line, has been met) and a presence of a "shoulder" in the histogram meeting the shape criterion mentioned by Buckland et al. (1993).

Fixed-width strip transect analysis. – To evaluate the effectiveness of strip-transects with varying cutoff distance, we calculated three density estimates using $\hat{D} = \frac{n}{2WL}$, where $\hat{D}$ is the density estimate, n the number of individuals sighted, L the length of the transect (i.e. 200 m) and $2W$ the width of the transect. Due to the limited visibility in the forest environment, the three cutoff distances from the line of observation were 5 m, 10 m and 20 m (i.e. strip-transect with width 10, 20 and 40 m respectively).

Throughout this paper, population density is reported as number of individuals per ha (± SE), and only applies for independent colugos.

RESULTS

The sampling regime yielded 34 observations of *Galeopterus variegatus.* The furthest observer-object distance was 21 m.

Fixed-width strip transect. – When constraining observations to 10 m wide strip transects, 61.8% of the observations (n = 21) were included and population density was estimated at 0.574 (± 0.145) ind/ha. Broader transects encompassed 85.3% and 100% of observations (20 and 40 m respectively; n = 29 and 34), and yielded density estimates of 0.396 (± 0.079) and 0.232 (± 0.050) ind/ha. From these transects, population estimates of colugo in the 2007 ha of forests in Singapore ranged from 466 to 1152 (Table 1).

Distance-sampling. – As indicated above, we removed the furthest 5% of the sightings to truncate our data. This resulted in a reduction from 34 sightings to 32.

The uniform key function adjusted with cosine series expansion (also known as the Fourier series model) possessed the lowest AIC score and produced a population density estimate of 0.535 (± 0.104), with an effective strip width of 8.17 m (see Table 2). Additionally, the coefficient of variation for this model was < 20% and therefore was deemed to be reasonably precise, as suggested by Buckland et al. (1993). The detection probability function of the Fourier series model (Fig. 1) showed a "shoulder" and implied that there was no evasive behaviour exhibited by the subject. It was also noteworthy that the density estimates obtained by the other models were very similar to that by the Fourier series model, differing by less than 5%. Using the most parsimonious model, we estimated that the colugo population was 1074 (± 209) individuals in the 2007 ha of protected lowland forest of Singapore.

DISCUSSION

To the best of our knowledge, this is the first study to investigate the suitability of various forms of line transect methods for assessing population density of *G. variegatus* in tropical forests.

Fixed-width strip transect. – As no other studies have compared methods for estimating the population density of colugos, the appropriate strip width that should be used is not clear. Because use of an incorrect cutoff distance can lead to gross deviation from the true population density, we provided a range of cut-off distances for the analysis of fixed-width strip transect (see National Research Council, 1981).

From the results, it was evident that with each doubling of the area covered by the strip transect (i.e. from 10 m width to 20 m, and from 20 m width to 40 m), the number of observations did not increase correspondingly (i.e. from 21 to 29 to 34, respectively). This likely reflects rapid reduction

Table 1. Estimated population density ($\hat{D}$) of Sunda Colugos (*Galeopterus variegatus*) and total population size in Singapore (2007 ha) using fixed-width strip transects.

Parameters	Width of Fixed Transect 10 m	20 m	40 m
Number of observations	21	29	34
$\hat{D}$ (+/- S.E.)	0.574 (± 0.145)	0.396 (± 0.079)	0.232 (± 0.050)
Estimated population size	1,152 (± 291)	795 (± 159)	466 (± 100)
C.V.	25.3%	19.9%	21.6%

in visibility with distance. As colugos are cryptic species and rarely vocalise, the only mode of detection is by visual cues, especially the strong eye-shine during spotlighting. Thus, within the complex three-dimensional space of tropical forests, it is expected that visibility is reduced drastically with increasing distance, leading to disproportional decrease in detection probability.

As a result, it is most likely that the density estimates from the larger fixed-width strip transects under-estimated colugo numbers. Consequently, we argue that the most appropriate strip transect used here was the narrowest, 10 m. This was supported by distance-sampling procedures, which indicated that the effective width of variable-width methods was approximately 8 m (see below).

Distance-sampling. **–** The presence of a "shoulder" in the detection probability function (Fig. 1) indicates that the Sunda Colugo was not exhibiting evasive behaviour (characterised by a peak in observations away from the line transect). These data agree with our observations that colugos normally do not behave adversely to human presence, regardless of day or night. Even though colugos are capable of gliding away from approaching humans, they often continued with their activities and tolerated further approach and visual observation, provided that a weaker flashlight was used for illumination after the initial encounter. This absence of evasive behaviour may be attributed to the apparent lack of hunting in Singapore. Thus, it is probable that observations made during this study were at their initial positions, thus meeting a key assumption.

We made extra effort to scan for colugos near the line transect. However, we could not confirm full detection along the line transect in this study, which is another assumption in distance-sampling method (and also for the fixed-width line transect method; see below). We believe that in the three-dimensional space and density of tropical rainforests, full detection of arboreal species can be attained only by sampling at all possible heights (up to 45 m in tropical lowland rainforests) and is practically impossible for most studies. Nevertheless, we are confident that we detected most, if not all, colugos near the transect line because during their active period (from 2000 to 2359 hours), colugos exhibit increased activity (e.g. foraging along tree branches) which aid in the detection of their presence. Additionally, spotlighting during the night also enhanced the detection of colugos by making use of their eye-shine, an additional cue of their presence, from distances up to 43 m (unpublished data). Despite these arguments in favour of our sampling, density estimates provided here should be treated conservatively, as numbers may be higher than we were able to document.

Although Buckland et al. (1993) recommended a minimum of 40 sightings for the calculation of reliable population densities, the selected model produced from distance-sampling of 32 sightings (i.e. the Fourier series model) possessed a coefficient of variation lower than 20% and was thus deemed to be reasonably precise, as suggested by Buckland et al. (1993). In addition, the other models possessed a coefficient of variation slighter greater than 20% (Table 2) but also yielded density estimates with a difference of less than 5%. We therefore felt confident that the data presented here yielded consistent and reasonably precise estimates with the various options of modeling.

Comparison of the two methods. **–** When comparing results of the two methods, the 10m-wide strip transect produced an estimate that is 7.3% greater than that by the best distance-sampling model. Even though both approaches utilised the same dataset in this study, the former disregarded observations beyond the transect boundary while the latter incorporated 95% of the sightings after truncation for the modeling of

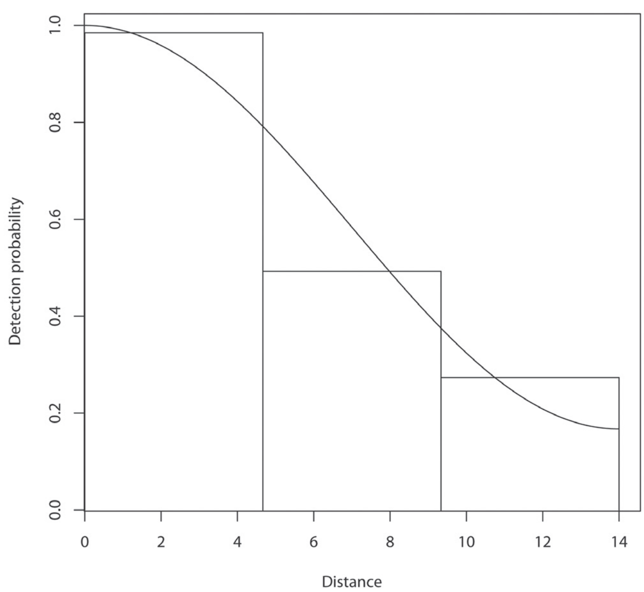

Fig. 1. The detection probability function of the Fourier series model after removing the extreme 5% of observations.

Table 2. Estimated population density ($\hat{D}$) of Sunda Colugos (*Galeopterus variegatus*) in Singapore using distance-sampling analysis. Estimates determined using program DISTANCE. Presented are density estimates, effective strip width (ESW), 95% confidence interval (95% C.I.), coefficient of variation (C.V.) and AIC values.

Parameters	$\hat{D}$ (± S.E.)	ESW	95% C.I.	AIC	ΔAIC	C.V.
Uniform + cosine series	0.535 (± 0.104)	8.17	0.366-0.783	160.95 *	0	0.194 **
Half-normal + cosine series	0.541 (± 0.115)	8.08	0.357-0.820	161.51	0.56	0.212
Half-normal + Hermite	0.541 (± 0.115)	8.08	0.357-0.820	161.51	0.56	0.212
Hazard-rate + cosine series	0.554 (± 0.150)	7.89	0.326-0.942	161.89	0.91	0.270
Uniform + simple polynomials	0.535 (± 0.116)	8.17	0.350-0.819	162.74	1.79	0.217

* denotes lowest AIC values; ** denotes C.V. < 0.200.

the detection probability function. Thus, the fixed-width strip transect method excludes data which are potentially informative, possibly resulting in the slight difference in density estimates obtained.

Importantly, the coefficient of variation of the 10 m fixed-width strip transect was much greater than that of the variable-width model. Thus, by making use of the additional sightings to model the detection probability function, distance-sampling is likely to be more precise and thus more sensitive to changes in population densities. This advantage in greater precision is not the result of additional sampling as similar effort was invested for both methods (i.e. the same amount of time and distance covered), with the exception that sightings further than 5m from transect line were disregarded for the fixed-width strip transect. As such, we believe that distance-sampling is a more appropriate method for long-term monitoring of colugo populations in forested habitats.

General discussion. – Most transect surveys of arboreal mammals have been of primates (e.g. Nijman et al., 2005), and were not without criticisms. First, there are few sites whereby primates are not disturbed or hunted by humans. As such, most primates are wary of human presence and exhibit evasive behaviour upon contact, thereby violating one of the important assumptions in distance-sampling (Marshall et al., 2008). Additionally, most primates are gregarious and occur in social groups of several to as many as a few hundred individuals (Barton et al., 1992, Swindler, 1998). Therefore, it may be difficult to ascertain the group spread and thus measure the exact distance from transect to the centre of the group, violating another important assumption (Marshall et al., 2008).

The above-mentioned issues do not seem to be relevant to colugos. As discussed earlier, evasive behaviour likely was absent in this study, probably because of the lack of hunting in Singapore. Furthermore, colugos are normally encountered singly (with the exceptions of female colugos with their young on their undersides) and the distance to the individuals, rather than group centroids, was used for the distance-sampling. As a result, although the Sunda Colugo, like most primates, is arboreal, there is no clear violation of the assumptions in distance-sampling.

Density estimates reported here compare well with those obtained at the Singapore Zoo and Night Safari, where Agoramoorthy et al. (2005) reported 0.550 ± 0.078 and 0.601 ± 0.078 ind/ha respectively. The Singapore Zoo (about 28 ha) and the Night Safari (about 40 ha) are located within the Central Catchment Nature Reserves and there is contiguous vegetation connecting the localities. Although vegetation at the Singapore Zoo was landscaped to a large extent, the high density of mature trees constitutes a semi-open landscape which resembles the structure of a tropical secondary forest. Furthermore, the great diversity of native and non-native trees planted within the compound might also prove to be attractive for colugos, as colugos are generalists and feeds on leaves from a large variety of plant species (Wischusen et al., 1998, Agoramoorthy et al., 2005). In contrast, the Night Safari consists of secondary rainforest vegetation of the Central Catchment Nature Reserve with minimal landscaping. Although the observers performing the sampling were different in these two studies, distance-sampling still yielded similar population density estimates for the two small plots of semi-artificial landscape that are nested within the study site of this study (i.e. the Central Catchment Nature Reserve).

Therefore, we are confident that our study provided sufficient evidence that distance-sampling is a suitable technique for the long-term monitoring of Sunda Colugo in the complex three-dimensional space of tropical rainforests.

Future of* Galeopterus variegatus *in Singapore. – We estimated that 1,074 ± 209 individuals exist within the 2007 ha of protected forests in Singapore (i.e. Bukit Timah Nature Reserve and Central Catchment Nature Reserve). Boinski et al. (1998) argued that local extinction of similar-sized and arboreal neotropical squirrel monkeys (*Saimiri* spp.) was almost certain when group size dropped to less than 15 members and had less than about 30 hectares of available habitat. If this is a valid comparison, it suggests that colugos in Singapore constitute a healthy and almost certainly viable population, both in terms of population numbers and amount of available habitat. Nevertheless, we stress that proper baseline data (e.g. lifespan and fecundity) for a detailed population viability analysis (White, 2000) is currently not available for the colugos.

In Singapore, colugos can be reliably found only from the Central Catchment Nature Reserve and Bukit Timah Nature Reserve thus far. While there were unsubstantiated sightings from Khatib Bongsu (S. Rajathurai, pers. comm.) and small peripheral populations outside the central catchment area (e.g. the German European School at Bukit Tinggi; Yeo & Lim, 1992), these sites have been surveyed and there is no indication that colugos are present in any substantial numbers.

In the recent years, however, there have also been confirmed sightings of colugos at the Bukit Batok Nature Park (T. T.

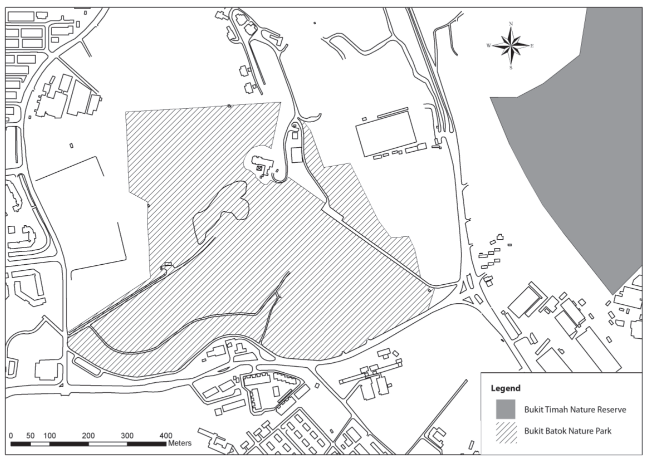

Fig. 2. Map showing the separation between Bukit Timah Nature Reserve and Bukit Batok Nature Park (location with new sightings of Sunda Colugo).

Guttensohn, Y. Cai, pers. comm.). This park is 36 ha and has remnant forests which are separated from the edge of Bukit Timah Nature Reserve by a road (Fig. 2). Given the colugo's ability to glide up to 136 metres, even crossing roads (Lim, 2007), expansion to the latter reserve is reasonable and is a piece of positive evidence that the colugo is likely to persist in the remaining forests of Singapore.

Conclusion. **–** The present study focuses on the tropical forests in Singapore — which is a heterogeneous matrix of different forest types, with mature secondary forest being the biggest component (ca. 77%). Although the population density obtained in this study may not be applicable to other pristine sites in the animal's range, we are confident that distance-sampling has the potential to be a standard protocol for colugo population estimation. While colugos are likely to persist in Singapore, this scenario is contingent on the continued existence of tropical forests in land-scarce Singapore as current knowledge about its ecology suggests that it is strictly a forest-dwelling animal. With many of the large- and medium-sized mammals extirpated from the forests of Singapore, the charismatic but enigmatic Sunda Colugo has the clear potential to be a flagship species for the conservation scene in Singapore.

ACKNOWLEDGEMENTS

We thank the National Parks Board for permission to conduct fieldwork in the Nature Reserve of Singapore. Special thanks to: Benjamin Lee, Rachel Lim, Ping Ting Chew and many other staff at National Parks Board; Douglas Kelt, Sara Krause, Kelvin Lim, Jaya Smith for constructive discussions; and all the volunteers, especially Kwok Wai Chan, Lena Lim and Alan Yeo. We also thank Yixiong Cai, Teresa Guttensohn and Subaraj Rajathurai for the additional sightings, and are grateful for the financial support provided by National University of Singapore.

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