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AKDE$_C$ home range size and habitat selection of Sumatran elephants

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Abstract

Context. Understanding ranging behaviour and habitat selection of threatened species is crucial for the development of conservation strategies and the design of conservation areas. Our understanding of the actual needs of the critically endangered Sumatran elephant in this context is insufficient.

Aims. Provide reliable subspecies-specific information on home range size and habitat selection of Sumatran elephants.

Methods. Using both the new area-corrected autocorrelated kernel density estimation (AKDE$_C$) and two commonly applied conventional methods, the home range sizes of nine Sumatran elephants were estimated. Elephant habitat selection was studied using Manly's selection ratios.

Key results. AKDE$_C$ home ranges of adults ranged from 275 km^2 to 1352 km^2. Estimates obtained using conventional KDE and minimum convex polygon (MCP) ranged between 156 km^2 and 997 km^2. Overall habitat selection was significant for both slope and land-cover type, whereas individual preferences varied to some extent. On the basis of global selection ratios, we found natural forest, pulpwood plantations and gentle slopes ($\leq 4°$) to be significantly selected, whereas most areas affected by human activities and steeper slopes were avoided by the majority of animals included in the study.

Conclusions. As expected, AKDE$_C$ estimates were much larger than those obtained using conventional methods because conventional methods have a tendency to underestimate home range size when confronted with autocorrelated movement data and produce estimates that refer to the limited study period only, whereas AKDE$_C$ estimates include the predicted animal's long-term space use. The extremely large AKDE$_C$ estimate obtained for a subadult male most likely represents a combination of population dispersal range and temporary home range rather than its final adult home range. Regardless, it appears that Sumatran elephants roam over much larger areas than previously assumed. Natural forests and relatively flat areas are of great importance for Sumatran elephants. The observed intensive use of pulpwood plantations by one individual is likely because of limited availability of alternative suitable habitats.

Implications. A landscape-wide approach to elephant conservation that takes large home ranges into account, is required, and should include forest protection and restoration and elephant friendly management of existing pulpwood concessions, with special focus on areas with relatively gentle slopes.

Additional keywords: area-corrected autocorrelated kernel density estimation, Asian elephant, Bukit Tigapuluh, elephant conservation, *Elephas maximus sumatranus*, habitat preference, movement behaviour, ranging behaviour, resource selection.

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Introduction

The critically endangered Sumatran elephant (*Elephas maximus sumatranus*; Gopala *et al*. 2011) is one of three currently recognised subspecies of Asian elephants (Shoshani and Eisenberg 1982; Choudhury *et al*. 2008) and is both genetically (Fleischer *et al*. 2001) and anatomically (Shoshani and Eisenberg 1982) different from other Asian elephants. On the basis of mtDNA analysis, Sumatran elephants form a monophyletic group (Fleischer *et al*. 2001) that can be considered an evolutionary signification unit (ESU), underlining the importance of the protection of the remaining wild populations in Indonesia (Blake and Hedges 2004; Hedges *et al*. 2005). However, in addition to general challenges, such as limited conservation resources and land use conflicts, the conservation of the Sumatran elephant is also hampered to some extent by a lack of sound information, making it difficult to design subspecies-specific conservation strategies, conservation areas and interventions. Even basic reliable information on elephant distribution and population status is not available for most of Sumatra (Blake and Hedges 2004; Hedges *et al*. 2005; but see Moßbrucker *et al*. 2015). In addition to population data, site managers also require sound knowledge on ranging behaviour and habitat requirements, so as to be able to adequately design and manage the areas inhabited by elephants. Whereas other subspecies of the Asian elephant are comparatively well studied in this regard (see Sukumar 2003 for a detailed overview), information on habitat selection and home ranges and, thus, our understanding of the actual needs of Sumatran elephants concerning habitat size and composition, is presently insufficient, with available data being limited to the results of one study of a female elephant in Bengkulu province (Sitompul *et al*. 2013*a*, 2013*b*) and a study based on presence-only data conducted in Aceh province (Rood *et al*. 2010).

Understanding the ranging behaviour of animals is of considerable importance for conservation planning, and the study of the animal home range (Burt 1943; Powell 2000; Powell and Mitchell 2012; Fleming *et al*. 2015) is of special interest in both theoretical and applied ecology (Sukumar 1992; Fleming *et al*. 2015). However, low natural elephant density and the elusive nature and dense habitat of forest elephants pose logistical and methodical challenges, which may partly explain the scarcity of available studies. Fortunately, advances in monitoring technology over the past decades have greatly enhanced the scientific toolkit and, today, modern satellite GPS collars can collect accurate and continuous animalposition data over extended periods of time, without requiring direct sightings or telemetry by field teams (Ropert-Coudert and Wilson 2005; Wall *et al*. 2014). However, data analysis remains challenging because of inherent autocorrelation of movement data that negatively affects most conventional home range estimators (Hansteen *et al*. 1997; Rooney *et al*. 1998; Boyce *et al*. 2010; Fleming *et al*. 2015), including the commonly applied kernel density-estimation (KDE) method (Worton 1989). Autocorrelation in animal tracking data stems from the fact that observations sampled closely in time are necessarily located closely in space. When subsequent locations are strongly related to each other, they provide only marginal information regarding the home range area. Methods that ignore autocorrelation, therefore, overestimate the information content and effective sample size of the data. Simple geometrical methods such as the minimum convex polygon (MCP; Hayne 1949) are less prone to failure but equally unsatisfactory, because they are limited to the estimation of a crude home range outline and largely ignore the information provided by data from within the MCP itself (see Powell 2000 for a critical review). Fortunately, many problems and limitations in home range estimation were overcome by the recently developed autocorrelated KDE (AKDE) that can handle large autocorrelated movement datasets without the need of thinning the data or excluding inherent information from the data structure (Fleming *et al*. 2015). AKDE is the generalisation of the well understood Gaussian reference function KDE method, whereby the bandwidth optimisation relations are derived under the assumption of autocorrelated data rather than IID data. AKDE makes no particular assumptions about the data; however, to account for autocorrelation, AKDE does require an estimate of the autocorrelation structure of the data, which can be calculated by fitting a movement model to the data. AKDE outperforms conventional KDE for autocorrelated datasets and returns the same results as would have been obtained with KDE when autocorrelation is absent (see Fleming *et al*. 2015 for a detailed discussion). The area-corrected $AKDE_C$ method further improves the AKDE by correcting for small sample-size biases in area estimation (Fleming and Calabrese 2016), making $AKDE_C$ currently the most suitable tool for animal home range analysis.

In addition to home range estimation, movement data can also provide valuable insights into animal resource selection if meaningful covariates have been measured *a priori*. Understanding resource selection of animals can be of great importance for conservation and management (Manly *et al*. 2002; Kertson and Marzluff 2011). There are various methods available to study resource selection but most involve the analysis of a combination of used, available, and unused resource units (see Manly *et al*. 2002 for a comprehensive overview). If these resources can be defined by distinct categories, selection can be estimated, *inter alia*, using selection ratios, a special type of resource selection function that compares the actual ratios (e.g. used vs available) of distinct resource units with the probability of these units being used (Manly *et al*. 2002). Being comparatively easy to apply and to interpret, this straightforward approach is among the most commonly applied methods (Manly *et al*. 2002).

We here report $AKDE_C$ home range estimates for nine Sumatran elephants and present information on elephant habitat selection in Bukit Tigapuluh, Indonesia. In addition to $AKDE_C$, conventional KDE and MCP home range estimates are provided to allow the comparison of our results with older studies.

Materials and methods

Study site

The study was conducted in Bukit Tigapuluh (Fig. 1), a more than 3500-km^2 large landscape located in the geographical centre of the Indonesian island of Sumatra (1°4′27.72″S, 102°30′43.89″E). Bukit Tigapuluh stretches over two provinces (Riau and Jambi) and includes a 1440-km^2 large National Park that is inhabited by the native tribe of the Talang Mamak people (Pratje and Sitompul 2009). Large parts of the landscape have been converted into various land-use types, displacing the species-rich lowland rainforest that is now largely limited to rugged or remote areas (Frankfurt Zoological Society, unpubl. data 2005–15). The archetype closed-canopy forest is characterised by the Dipterocarpaceae family (111 species are found in Sumatra), with emergent trees reaching up to 70 m (e.g. *Dipterocarpus* spp., *Parashorea* spp., *Shorea* spp., *Dryobalanops* spp.). Other commonly found tree families include Caesalpiniaceae, Burseraceae, Sapotaceae, Euphorbiacae, Rubiaceae, Annonaceae, Lauraceae, Moraceae (Ficeae) and Myristicaceae (Whitten *et al*. 1999). Open areas and grassland are rarely found within the forest, and, if present, are largely limited to cultivated land (e.g. recently opened fields and plantations) or heavily disturbed areas (e.g. burned patches). The main cash crops planted in the area are rubber trees (*Hevea brasiliensis*) and oil palms (*Elaeis guineensis*), and

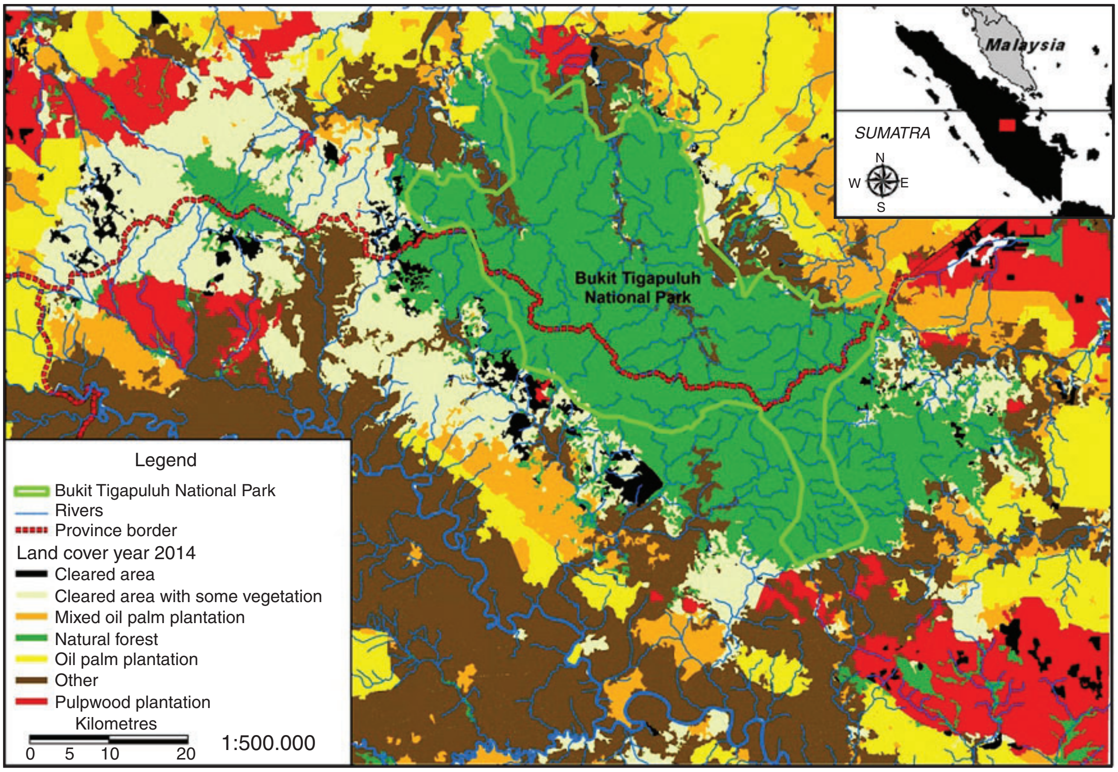

Fig. 1. Land-cover information for the year 2014, Bukit Tigapuluh landscape, Sumatra, Indonesia. (Source: land cover: World Wide Fund for Nature (WWF) Indonesia and Setiabudi; rivers and administrative boundaries: Frankfurt Zoological Society and BAKOSURTANAL Indonesia).

both species are frequently targeted by crop-raiding elephants (Moßbrucker 2013). The climate is tropical, with year-round warm temperatures (mean annual temperature = 22°C, min = 21°C, max = 33°C) and high rainfall (average precipitation = 2577 mm year^{-1}, max = 347 mm month^{-1}, min = 83 mm month^{-1}), and the altitude ranges between 60 m and 843 m asl (Pratje and Sitompul 2009). With an estimated 143 elephants roaming the mostly unprotected areas south and west of the Bukit Tigapuluh National Park, this landscape supports the largest known elephant population in central Sumatra (Moßbrucker *et al*. 2015). A landscape-wide elephant-conservation program, including, *inter alia*, human–elephant conflict (HEC) mitigation, elephant monitoring and protection patrols, and habitat protection patrols, is implemented by Frankfurt Zoological Society (FZS) in cooperation with local wildlife conservation authorities (KSDAE Jambi) and the Bukit Tigapuluh National Park since 2010.

Elephant monitoring

Seven adult females, one adult bull and one subadult bull were monitored over different time periods between July 2012 and December 2015, using satellite GPS collars (Africa Wildlife Tracking, Pretoria, South Africa) that automatically recorded up to 12 positions per day for each animal. Females were randomly selected from all family groups encountered in the main elephant habitat (south and south-west of the Bukit Tigapuluh National Park). The adult bull was selected randomly among several known crop raiders, and the subadult bull was collared when he was translocated back to the core zone of the elephant habitat, after having killed a farmer in the eastern-most part of the landscape. GPS collars were exchanged up to three times for each individual in anticipation of battery exhaustion or to replace damaged units. Collaring was conducted by an experienced veterinarian who specialises in the treatment of both wild and captive Sumatran elephants, along with support by several state-employed elephant experts under the strict supervision of the Jambi division of the Indonesian department of Conservation of Natural Resources and Ecosystem (KSDAE, formerly BKSDA) and permission of the Indonesian Ministry of Forestry under research permits numbers 058/EXT/SIP/FRP/SM/XI/2011, 411/SIP/FRP/SM/X/2012, 90/EXT/SIP/FRP/SM/XII/2013 and 85/SIP/FRP/SM/IV/2015 issued by the Indonesian State Ministry of Research and Technology (RISTEK). A mixture of xylazine (ILIUM XYALZIL-100 (100 mg xylazine per 1 mL), Troy Laboratory, Glendening, NSW) and ketamine (KETAMIL (100 mg ketamine per 1 mL), Troy Laboratory) (~2.5 : 1) was used for sedation. All movement data were managed and stored in Movebank (Wikelski and Kays 2015).

Home range analysis

Ninety-five per cent AKDE$_C$ home ranges were calculated using R 3.3.1, package ctmm 0.3.2 (Calabrese *et al*. 2016; Fleming and Calabrese 2016; R Core Team 2016), following Fleming *et al*. (2015). After visualising the autocorrelation structure to obtain starting values for the variance and autocorrelation timescales, we fitted three different continuous-time movement models, including independent and identically distributed (IID), Ornstein–Uhlenbeck (OU, including autocorrelation in location; Dunn and Gipson 1977) and Ornstein–Uhlenbeck-F (OUF, including autocorrelation in both location and velocity; Fleming *et al*. 2014) to each individual elephant dataset. From these three models, we selected the one with the best fit by comparing second-order Akaike information criterion (AIC_C; Burnham and Anderson 2002) values and then proceeded with the calculation of $AKDE_C$ home ranges and confidence limits.

Conventional KDE home ranges were estimated for 95% utilisation distributions, with the bandwidth (*h*) selected using the least square cross-validation method (LSCV; Seaman and Powell 1996; Seaman 1999). So as to reduce autocorrelation while maintaining a sufficient number of relocations (≥50; Seaman 1999), we cropped our dataset to one random relocation every third day before conducting KDEs. MCPs were obtained for all individuals by using the full dataset. Both KDE and MCP were calculated using R 3.3.1, package adehabitatHR 0.4.14 (Calenge 2006; R Core Team 2016).

Habitat selection analysis

Habitat selection was studied using selection ratios following Manly *et al*. (2002). A 'design III' study (*sensu* Thomas and Taylor 1990) was used with both the available and the used habitat units measured for each animal separately and the available areas defined by the 95% AKDE home ranges. The elephant referred to as Haris was excluded from further analysis because a reliable adult home range could not be estimated because of his unique behaviour (discussed below). Analysis was conducted using R 3.3.1, package adehabitatHS 0.3.12 (Calenge 2006; R Core Team 2016), on the basis of subsamples consisting of one random relocation per day (to adjust for unequal sampling schedules among tags), with usage defined as the percentage of relocations within each distinct habitat class. After using log-likelihood chi-square goodness-of-fit tests (χ_L^2) to test for both significant overall selection and habitat selection of individual animals, Manly selection ratios ($\hat{w}$) were estimated and Bonferroni confidence intervals (Cl_{low}, Cl_{up}) calculated. Habitat classes used more often than expected (implying preference) were indicated by $\hat{w} > 1$, with a significance level of $CI_{low} > 1$, and habitat classes used less frequently than expected (implying avoidance) were indicated by $\hat{w} < 1$, with a significance level of $Cl_{up} < 1$.

Two separate analyses were conducted, focusing on land-cover type and slope respectively. On the basis of 8 years of field observations by the author, both of these two factors were expected to significantly influence elephant movement behaviour in Bukit Tigapuluh and play an important role in landscape management and conservation planning. Two datasets were compiled by classifying the available habitat into distinct categories on the basis of land-cover maps provided by the World Wide Fund for Nature (WWF; remote sensing by Budi Setiabudi and WWF Indonesia using Landsat 7 and Landsat 8 satellite images; Fig. 1) and slope-value maps derived from Shuttle Radar Topography Mission (SRTM) data (digital elevation model with a resolution of 1 arc-second, courtesy of the USA Geological Survey, USGS). Land cover was classified into seven distinct categories (Table 1). Slope values were compiled into one-degree steps and, subsequently, grouped into five classes as follows: S1 = slope values (SV) ≤ 4°, S2 = SV 5–8°, S3 = SV 9–12°, S4 = SV 13–16° and S5 = SV > 16°. Because land cover in Bukit Tigapuluh is likely to be subject to considerable change, we limited the time frame for analysis involving land-cover types to the year 2014 for which we could obtain reliable maps instead of considering the entire study period. Thus, only five animals were included into land-cover selection analysis, the remaining three animals having no relocations in 2014. Analysis not involving land-cover types was conducted over the entire study period, including eight elephants. All spatial data were prepared and compiled using both QGIS Desktop 2.10.1 (Quantum GIS Development Team 2015) and ArcMap 9.3 (ESRI 2008).

Results

Elephant monitoring

The monitoring of nine elephants over periods of 334–1232 days resulted into 570–10 252 GPS-position records available for analysis for each individual (Table 3). All GPS collars provided fairly regular position updates, with the exception of Elena's unit, which uploaded data less frequently than scheduled. Direct observations and radio-telemetry confirmed that Elena's collar was attached correctly and provided accurate position information (A. M. Moßbrucker, pers. obs.), with the technical problem being apparently limited to the subunit of the GPS collar that handles the data upload to the Iridium satellite network.

Home range estimation

Area-corrected autocorrelated kernel density estimates ($AKDE_C$) were obtained for all nine elephants (Fig. 2, Table 3), with the model OUF performing best for all but one individual (Dadang; Table 2), for which the OU model reached a slightly smaller $AKDE_C$ value, most likely owing to the more tortuous movements observed for this particular animal. As expected, the autocorrelated models returned consistently substantially smaller $AKDE_C$ values than did the uncorrelated null model

Table 1. Classification of land-cover types present within the elephant range in the Bukit Tigapuluh landscape, based on satellite imagery
Data source: World Wide Fund for Nature (WWF) Indonesia

Land cover type classes	Description
CA	Cleared areas (barren land)
CV	Cleared areas with some vegetation (e.g. grass and shrubs)
MP	Mixed oil palm plantation (patchwork of oil palms (*Elaeis guineensis*) and other land-cover types or crops)
NF	Natural grown forest (mostly secondary forest)
OP	Oil palm plantation (continuous monoculture patches)
OT	Other types (mostly rubber tree (*Hevea brasiliensis*) plantations, but also including all those land cover types not specifically classified or not identifiable)
PP	Pulpwood plantation (monoculture of either *Acacia* spp. or *Eucalyptus* spp.)

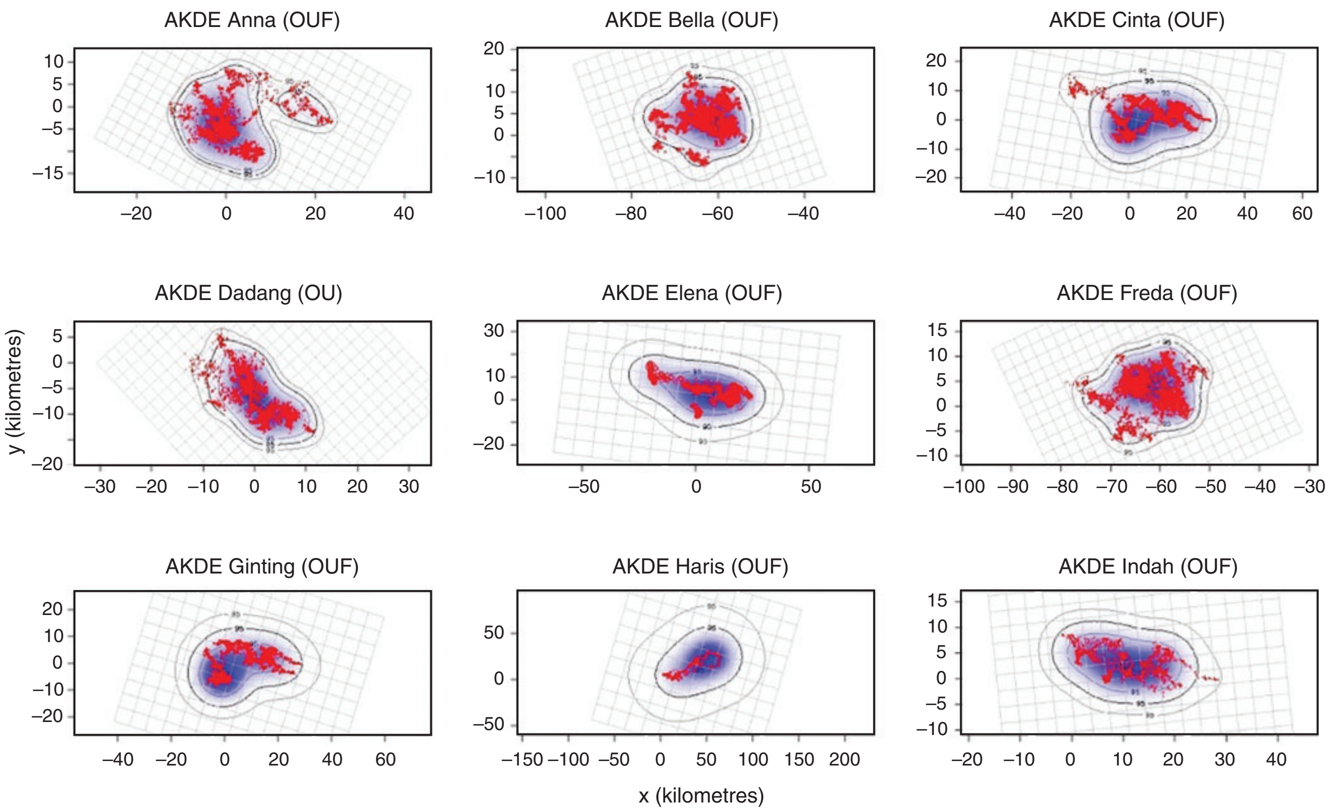

Fig. 2. Illustration of the area-corrected 95% autocorrelated kernel density estimation ($AKDE_C$) home ranges of nine Sumatran elephants (bold outline), including lower and upper confidence limits of the estimates. GPS data points used for analysis are shown as red dots. Estimates with wide confidence intervals that extend beyond the data are projecting additional future space use relative to what has been observed in the limited sample, with grid lines roughly corresponding to the resolution of the kernel density estimate.

Table 2. Continuous-time movementmodel selection for area-corrected autocorrelated kernel density estimation ($AKDE_C$) using the difference in the for finite sample sizecorrected Akaike information criterion (ΔAIC_C) among the three models IID, OU and OUF

The effective number of degrees of freedom in the area estimate from the Gaussian reference function approximation (DOF area) are shown in parentheses

Animal	ΔAIC_C IID (DOF area)	ΔAIC_C OU (DOF area)	ΔAIC_C OUF (DOF area)
Anna	121489.8 (10215)	1361.3 (21.87)	0 (30.20)
Bella	17198.4 (1911)	212.8 (11.58)	0 (16.94)
Cinta	137965 (10251)	1952.3 (8.19)	0 (14.51)
Dadang	79811.8 (8095)	0 (32.54)	2 (32.58)
Elena	6127.56 (569)	96.74 (5.67)	0 (7.39)
Freda	95317.8 (9039)	1577.3 (23.14)	0 (36.03)
Ginting	105269 (7797)	1128.5 (6.46)	0 (8.85)
Haris	67234.3 (4267)	701.2 (1.94)	0 (2.24)
Indah	38584.3 (3521)	965.3 (7.02)	0 (13.70)

(IID; Table 2). The 95% $AKDE_C$ area estimates for males ranged from 275 km^2 (Cl_{low} = 189, Cl_{up} 378) for adult bull Dadang, to an extreme 5180 km^2 (Cl_{low} = 745, Cl_{up} 13824) for subadult bull Haris. For females, $AKDE_C$ estimates ranged between 356 km^2 (Cl_{low} = 249, Cl_{up} 481; Freda) and 1352 km^2 (Cl_{low} = 560, Cl_{up} 2487; Elena). Calculated on the basis of a reduced dataset of 50–234 relocations per animal (Table 3), 95% KDE home ranges were with 156 km^2 (Dadang) to 380 km^2 (Cinta) generally substantial smaller than were the results of $AKDE_C$. Being slightly larger than the KDE estimates, the MCP home ranges ranged between 211 km^2 (Indah) and 997 km^2 (Haris; Table 3).

Habitat selection analysis

The proportions of available resource units differed substantially among individual animals, reflecting a multifaceted landscape (Tables S1, Table S2, available as Supplementary material to this paper). Overall, selection was significant for both slope ($\chi_L^2 = 79.76$, P-value = 0.0000) and land-cover type ($\chi_L^2 = 127.87$, P-value = 0.0000), but the test results were not homogenous, with land-cover type selection being significant for four of five elephants, and slope selection being significant for four of eight animals (Table 4). Global selection ratios were obtained for all habitat classes (Table 5). Mixed oil palm (MO), cleared areas with some vegetation (CV), other types (OT), cleared areas (CA) and oil palm (OP) were avoided, with the results for the latter two statistically significant. Both natural forest (NF) and pulpwood plantation (PP) were selected significantly more frequently than expected. The slope class S 1 was selected significantly more often than expected.

Table 3. Satellite telemetry period and home range estimates for nine Sumatran elephants using area-corrected 95% autocorrelated kernel density estimation ($AKDE_C$; including the 50% core range and confidence limits Cl_{low} and Cl_{up}), 95% kernel density estimation (KDE) and the minimum convex polygon (MCP) methods

n = number of relocations available for analysis

Animal, age (years)	Telemetry period	95% $AKDE_C$ {50% core range} **(Cl_{low}, Cl_{up})** [km^2]	95% KDE [km^2]	MCP [km^2]
Anna, >24 *adult* ♀	25 July 2012 – 8 Dec. 2015	460.89 {71.14} (311.41, 639.21) *n* = 10 216	247.26 *n* = 205	521.35 *n* = 10 216
Bella, >39 *adult* ♀	29 July 2012 – 16 June 2013	375.41 {89.45} (218.46, 574.15) *n* = 1912	295.74 *n* = 65	338.23 *n* = 1912
Cinta, >34 *adult* ♀	30 July 2012 – 8 Dec. 2015	972.46 {238.26} (538.19, 1533.06) *n* = 10 252	379.61 *n* = 234	624.26 *n* = 10 252
Dadang, ±29 *adult* ♂	31 July 2015 – 8 Dec. 2015	275.32 {67.02} (188.97, 377.67) *n* = 8096	155.58 *n* = 160	284.72 *n* = 8096
Elena, ±25 *adult* ♀	1 Aug. 2012 – 29 Dec. 2013	1352.09 {339.02} (560.17, 2486.91) *n* = 570	301.77 *n* = 50	548.45 *n* = 570
Freda, >22 *adult* ♀	30 July 2013 – 8 Dec. 2015	355.98 {90.42} (249.36, 481.28) *n* = 9040	257.66 *n* = 169	373.68 *n* = 9040
Ginting, >32 *adult* ♀	24 Jan. 2014 – 8 Dec. 2015	911.4 {243.20} (413.51, 1602.66) *n* = 7798	262.17 *n* = 137	453.59 *n* = 7798
Haris, ±13 *subadult* ♂	17 Nov. 2014 – 8 Dec. 2015	5179.54 {1275.83} (744.68, 13823.75) *n* = 4267	188.93 *n* = 78	997.10 *n* = 4267
Indah, >17 *adult* ♀	9 Jan. 2015 – 7 Dec. 2015	356.17 {92.73} (193.26, 568.05) *n* = 3522	186.78 *n* = 67	210.67 *n* = 3522

Table 4. Test results for habitat selection of Sumatran elephants using log-likelihood chi-square goodness of fit tests (χ_L^2) for two habitat characteristics, slope and land-cover type ($\alpha = 0.05$)

d.f., degrees of freedom

Animal	Slope			Land-cover type		
	χ_L^2	d.f.	*P*	χ_L^2	d.f.	*P*
Anna	1.19	4	0.8794	21.64	4	0.0002
Bella	0.61	3	0.8940	–	–	–
Cinta	14.43	4	0.0060	21.07	4	0.0003
Dadang	1.10	4	0.8944	7.88	5	0.1629
Elena	24.88	4	0.0001	–	–	–
Freda	1.59	3	0.6614	45.07	5	0.0000
Ginting	11.39	4	0.0225	32.21	4	0.0000
Indah	24.56	4	0.0001	–	–	–
Overall	79.76	30	0.0000	127.87	22	0.0000

Table 5. Global selection ratios ($\hat{w}$) of Sumatran elephants for seven land-cover type classes and five slope classes, with standard error (s.e.) and Bonferroni confidence limits (Cl_{low}, Cl_{up})

Habitat class	$\hat{w}$	s.e.	Cl_{low}	Cl_{up}
PP	2.49	0.20	1.96	3.01
NF	1.63	0.06	1.46	1.80
OT	0.77	0.11	0.46	1.07
CV	0.74	0.27	0.03	1.45
MO	0.67	0.24	0.04	1.31
CA	0.34	0.11	0.05	0.63
OP	0.14	0.08	0.00[A]	0.37
S 1	1.34	0.10	1.08	1.61
S 2	1.16	0.07	0.98	1.34
S 3	0.85	0.06	0.69	1.01
S 4	0.54	0.05	0.42	0.66
S 5	0.15	0.04	0.06	0.25

[A]An impossible negative confidence limit for OP has been replaced by 0.00.

Steeper slopes (≥4°) were avoided, with the results for slope classes S 4 and S 5 being statistically significant.

Discussion

Home range size

The present paper has described the first application of $AKDE_C$ for elephant home range estimation. The new home range estimator performed well for all but one animal, namely the subadult bull Haris, for which it was not possible to estimate a reliable $AKDE_C$ home range because of his unique movement behaviour. Asian elephant males leave their natal herd in the process of reaching adulthood, often dispersing from their mother's home range so as to explore adjacent habitat, which represents an important mechanism to decrease the risk of inbreeding (Sukumar 2003). Similar dispersal behaviour is also commonly observed in other large mammals, *inter alia*, tigers (*Panthera tigris*; Smith 1993), orangutans (*Pongo abelii* and *Pongo pygmaeus*; Delgado and Van Schaik 2000; Singleton and van Schaik 2001), brown bears (*Ursus arctos*; Jerina and Adamic 2008) or cougars (*Puma concolor*; Thompson and Jenks 2010). It appears that Haris has been undergoing this particular development phase during our observation period, with the extremely large $AKDE_C$ results likely reflecting a mixture of population dispersal range and temporary home range, rather than representing his final adult home range. Sometimes such streaking behaviour is obvious when an animal shifts its range; however, often dispersal is not visually obvious in location data. The fact that Haris' variogram does not asymptote is indicative that his dispersal phase is incomplete. The $AKDE_C$ estimate with its wide confidence intervals that extend beyond the data is projecting future space use relative to what has been observed in the limited sample. A cautious interpretation of Haris' $AKDE_C$ results based on the available section of his movement track would be that this animal will likely continue to explore the wider landscape in the near future before settling into a smaller adult home range, a behaviour that both KDE and MCP estimates fail to depict because these conventional methods lack any predictive component linked to the animal's movement behaviour.

Although generally substantially smaller than Haris' range estimate, all of the adult $AKDE_C$ home range estimates were still comparatively large. Certainly home range size varies among sites, individuals, and sometimes even among seasons, which may be due to several reasons such as, *inter alia*, food and water availability and distribution, social behaviour and human activity (Sukumar 1992, 2003). However, with the exception of studies that include seasonal migration and post-translocation movements, most published home ranges of Asian elephants range between 29.6 km^2 and 800 km^2 (e.g. Olivier 1978; Sukumar 1992; Baskaran *et al.* 1995; Weerakoon *et al.* 2004; Fernando *et al*. 2008; Alfred *et al*. 2012; Sitompul *et al*. 2013*a*). Although both the MCP and KDE estimates fit well into this commonly reported range, several of our $AKDE_C$ estimates were much larger, and $AKDE_C$ results for adults were ~2–4 times larger, than the corresponding conventional KDE estimates. Thus, there appears to be a general method-depending difference affecting the scale of the home range analysis outcomes, with the conventional KDE method apparently generating consistently smaller estimates than does the new $AKDE_C$ method. This outcome was expected, because the conventional methods, in addition to having the tendency to underestimate home range size when confronted with autocorrelated movement data, produce estimates that take account of the limited study period only (locations where the animal has been observed), whereas the AKDE method estimates the animal's long-term space use by including time-dependence movement information from the dataset (Fleming *et al*. 2015).

The only available estimate of home range size for Sumatran elephants is with just under 100 km^2 (Sitompul *et al*. 2013*a*) substantially smaller than even our most conservative results obtained by MCP and KDE analyses. Sitompul *et al*. (2013*a*) assumed that the small home range size of the monitored female may be a result of consistent food and water availability, in combination with the presence of human activities in the area that surrounds the confined habitat. Because their study used conventional methods to estimate home range size and both the monitoring period and number of individuals monitored were limited, we recommend the use of our $AKDE_C$ estimates as an orientation for conservation planning in Sumatra in cases where site-specific home range information is not available.

Habitat selection

Asian elephants are adaptive animals that persist in a variety of both natural and human-altered habitats (Sukumar 2003; de Silva and de Silva 2007), and, although they are most commonly found in forest ecosystems, they may also make intensive use of grass-land patches (English 2015), tallgrass floodplains (Steinheim *et al*. 2005) and other open or even tree-less areas (Sitompul *et al*. 2013*b*), and are known to exploit field crops and plantations across their range (e.g. Santiapillai and Jackson 1990; Sukumar 1992; Sukumar 2003). This general adaptability is reflected by our observations in Bukit Tigapuluh, where all available land-cover types and slope classes were used by elephants at least to some extent.

Although selection behaviour varied among individual animals, significant global results allowed us to draw some general conclusions concerning elephant habitat selection in our study area. Elephants in Bukit Tigapuluh showed a clear preference for natural forest, which is principally in accordance with Rood *et al*. (2010) that found Sumatran elephants in Aceh province to be largely confined to forested valleys with highly productive vegetation. These findings emphasised the importance of natural forests for elephants in Sumatra and illustrated the need to protect and restore the forest ecosystem within the elephant range, so as to bolster their conservation.

Unfortunately, in many parts of Bukit Tigapuluh, natural forest has been replaced by extensive pulpwood monocultures during the past decade. Interestingly, $\hat{w}$ was much larger for this substantially altered habitat than for natural forest, although pulpwood forests were used by only one of the animals included in the analysis (Freda). Freda's intensive use of pulpwood plantations is likely explained by the lack of alternatives within her range, with the few remaining fragments of natural forest (4.09% of her total home range size) being highly disturbed by human activities such as poaching, illegal gold mining and illegal logging, and the central pulpwood forest of Freda's core distribution being largely surrounded by guarded agriculture land (A. M. Moßbrucker, pers. obs.). Obviously, the comparatively disturbance-free pulpwood forests represent a vital refugium for elephants in this human-dominated part of the landscape. Similar observations were made in the Valparai plateau in southern India, where *Eucalyptus* and coffee plantations became important habitats in areas devoid of natural vegetation (Kumar *et al*. 2010).

Not surprisingly, cleared areas (CA) were significantly less often used than expected on the basis of availability and, therefore, are not likely to represent suitable habitat for Sumatran elephants, as has been noted previously (Sitompul *et al*. 2013*b*). However, oil palm monocultures (OP), the mostly rubber tree plantations containing miscellaneous category OT, and other agriculture areas that are still in transition to continuous plantations (MO, CV) were also avoided by elephants, although overall results were significant only for OP. This appears odd at first, given that crop raiding is, with 119–186 incidents per year, common (Frankfurt Zoological Society, unpubl. data, 2011–2015), and that oil palms and rubber trees are by far the most frequently destroyed crops in Bukit Tigapuluh (Moßbrucker 2013). However, these only superficially contradictive observations can be explained by the fact that although elephants may have learned to exploit agriculture areas, they are not tolerated there and many plantations and fields are guarded (A. M. Moßbrucker, pers. obs.). Therefore, elephants may not avoid fields and plantations *per se*, but may not be able to spend much time within agriculture land because of active crop protection, leading to an under-representation of these areas in the sample. Nevertheless, two monitored animals (Dadang and Anna) were able to use MO and CV more intensively than was expected on the basis of availability, which is likely to be due to an increased tolerance of both animals towards disturbances and the availability of shelter in the form of scrubland within both of these land-cover types.

Given the low percentage of the preferred natural forest within their home range, it is surprising that elephants are largely absent from the mostly forested Bukit Tigapuluh National Park that protects more than a third of the landscape (Moßbrucker 2009; Moßbrucker *et al*. 2015). It was assumed that steep slopes were at least partly responsible by hampering elephant movements, especially at the southern border of the national park (Moßbrucker 2009). On the basis of global selection ratios, we can confirm that Sumatran elephants appear to avoid steep slopes and favour flatter terrain, although log-likelihood chi-square goodness-of-fit test results were not statistically significant for all monitored animals. Similar behaviour was also observed for other mammal species (see, *inter alia*, Chiang 2007; Simcharoen *et al*. 2014; Dennison *et al*. 2016), aiming at minimising the costs of movement (Reichman and Aitchison 1981; Dickson *et al*. 2005). Although our findings make intuitive sense as a preference for gentle slopes, and easy terrain can be expected for energy efficiency (Wall *et al*. 2006), they do not necessarily indicate that elephant movements are principally constrained by slopes. Two cases of subadult bulls penetrating several kilometres into the rugged terrain of the southern park area were observed by the author within the past 6 years, with one case being well documented by the GPS collar data. Thus, our observations support the conclusions of others (Rood *et al*. 2010) that Sumatran elephants are principally capable of moving through steep terrain, although they may prefer flatter lowland areas. At this point, it remains unclear whether the park is simply too rugged to be attractive for elephants, or whether there are additional factors that keep the animals from moving into most parts of the protected area. Further research, including a thorough habitat suitability analysis (focusing on the extent and location of principally suitable elephant habitat within the national park boundaries), is therefore highly recommended.

Implications for conservation

Our results indicated that Sumatran elephants generally prefer gentle slopes and natural forest, and as a true landscape species, range over hundreds of square kilometres. These preferences must be taken into consideration when designing conservation areas and conservation strategies.

In Bukit Tigapuluh, all elephant home ranges included large percentages of agriculture areas and other land heavily affected by human activities, and HEC with all its associated negative consequences for both animals and people is common. Assuming that HEC can be contained only if elephants are able to satisfy their basic needs away from fields and human habitation and contact areas are minimised, the current situation may require the restructuring of the landscape and forest restoration in key areas so as to achieve harmonious human–elephant coexistence. Ecosystem restoration concessions represent a realistic option to restore natural forest even within designated production forest (Menteri Kehutanan 2004) and, thus, are a highly recommended land-use type for state-owned areas within the elephant range. Expanding existing wildlife areas by including adjacent forest concessions will not only benefit elephants, but also other landscape species such as Sumatran tigers (*P. t. sumatrae*), as has been noted previously (Imron *et al*. 2011).

In parts of the landscape where natural forest cannot be restored, pulpwood plantations may bolster elephant conservation, although carefully tailored management plans will be required so as to prevent elephant displacement during and just after pulpwood harvest. Conventional large-scale clear-cuts transform pulpwood plantations into barren land every 5–7 years, temporarily forcing resident elephants into adjacent areas, which will inevitably cause escalating conflicts with farming communities located in the surroundings and may ultimately jeopardise elephant survival. Negative impacts of harvesting could likely be mitigated to some extent by providing sufficiently sized alternative shelter and feeding grounds for elephants within concession areas and by implementing site-specific staggered harvesting protocols.

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