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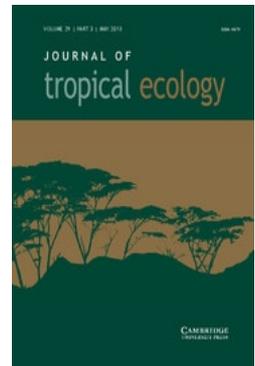
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The influence of the invasive weed *Lantana camara* on elephant habitat use in Mudumalai Tiger Reserve, southern India

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Abstract: Invasive weeds like *Lantana camara* have a range of effects on animals such as elephant. These plants are not edible by the Asian elephant (*Elephas maximus*). They also compete for space with elephant food plants and take over large areas of elephant habitat. We tested whether the addition of *L. camara* to a model consisting of measured environmental variables improved predictions of habitat use by elephant in Mudumalai Tiger Reserve, India. Elephant dung density was used to assess elephant habitat use from 62 line transects 1-km in length. Results indicated that habitat and impact of human settlements significantly influenced elephant habitat use at a landscape scale. However, we found no evidence for the hypothesis that the addition of *L. camara* significantly predicted elephant habitat use at the landscape level. We then tested the association of *L. camara* on elephant habitat use in the dry deciduous forest (DDF) where there was a significant interaction between DDF and *L. camara*. In the DDF, *L. camara* significantly predicted elephant habitat use. We conclude that while no significant effects of *L. camara* were seen at the level of an entire reserve, at a finer scale and in specific habitats negative effects of this invasive plant on elephant habitat use were observed.

Key Words: anthropogenic disturbance, *Elephas maximus*, elephant, habitat, invasive weeds, *Lantana camara*

INTRODUCTION

Invasive weeds are transformative, changing the character of natural ecosystems over substantial areas (Richardson *et al.* 2000) often resulting in homogenized biospheres of non-indigenous species (McKinney & Lockwood 1999). Empirical studies have shown that invasive weeds can negatively impact habitat selection and use by both wild and domestic ungulates (Hein & Miller 1992, Trammell & Butler 1995). For example, elk (*Cervus elephas nelsoni*) in Western Montana were attracted to habitats where the invasive knapweed (*Centaurea* spp.) had been removed (Thompson 1996). Invasive weeds compete with and replace native forage species (Belcher & Wilson 1989) thereby reducing the amount of food available to herbivores (DiTomaso 2000) through reduced forage production (Lym & Messersmith 1985).

One invasive weed of international significance is *Lantana camara* L., which was introduced to India from South America at the Indian Botanic Garden, Calcutta, as an ornamental plant in 1809 (Thakur *et al.* 1992). This widely invasive species grows particularly well in unshaded, anthropogenically disturbed habitat (Gentle & Duggin 1997, Sharma *et al.* 2005).

The Asian elephant (*Elephas maximus*) is a wide-ranging species traversing human-made administrative boundaries (Baskaran *et al.* 1995, Desai 1991). Humans have converted and developed forest habitat for agriculture or urban development (Desai & Baskaran 1996) making the conservation of large herbivores such as elephant challenging. In addition to illegal logging, cattle grazing, collection of fuel wood and non-timber forest produce, weed invasion appears to threaten many conservation areas including elephant habitat in the Nilgiri Biosphere Reserve, south India (Desai & Baskaran 1996, Silori & Mishra 2001).

Elephants are megaherbivores which require large amounts of forage to survive. The primary impact that

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L. camara has on elephant habitat is a reduction in grass cover. As *L. camara* spreads, grass cover declines and is replaced by *L. camara* because both vie for the same space (Wilson, unpubl. data). This reduction may be most pronounced in dry deciduous forest (DDF) where grass is the dominant food source for elephants and where elephant density is highest in the dry season (Sivaganesan 1991, Sivaganesan & Johnsingh 1995).

In this study, we examined the influence of *L. camara* on habitat use by elephant at the landscape level and within habitat in Mudumalai Tiger Reserve, southern India. The following hypotheses were tested: (1) the addition of *L. camara* significantly predicted elephant habitat use across habitats at the landscape level; (2) models containing *L. camara* better explained elephant habitat use across habitats using an information-theoretic approach; (3) finally, because our results indicated a significant interaction between the DDF and *L. camara*, we tested whether *L. camara* significantly influenced habitat use by elephant within the DDF at a lower spatial scale.

METHODS

Study site and methods

Mudumalai Tiger Reserve (hereafter Mudumalai; 11°32'–11°42'N, 76°20'–76°45'E) includes 321 km² of plains and foothills of the Nilgiri district in Tamil Nadu state, southern India. The reserve is bounded to the north by Bandipur Tiger Reserve and to the west and north-west by Wynaad Wildlife Sanctuary. Singara and Sigur Reserve forests form Mudumalai's southern and eastern boundaries (Figure 1a). Mudumalai and its surrounding reserves are part of the 5500-km² Nilgiri Biosphere Reserve (NBR) (Sukumar *et al.* 2004). The wild elephant population in Mudumalai ranges from approximately 350 to 1000 elephants depending on seasonal movement of elephants across the NBR (Baskaran *et al.* 2010a, Daniel *et al.* 1987).

Tropical forest types in Mudumalai include moist deciduous, dry deciduous (mixed and *Shorea* vegetation) and thorn forest (Champion & Seth 1968) (Figure 1a). *Tectona grandis* plantations and native trees were commercially logged in Mudumalai from the beginning of the 19th century and continued until the 1980s (Srivastava 2009). The presence of *L. camara* was described as a problem to the dry deciduous forest and *T. grandis* plantations in Mudumalai, Benne and Theppakadu blocks of Mudumalai in 1941 (Ranganathan 1941).

Field observations and measurements were conducted between January and May 2009, and November 2009 and May 2010 to estimate elephant dung density and habitat assessments. A topographic map (1 : 50 000) of

Mudumalai derived from ground surveys was divided into 94, 2 × 2-km cells using MapInfo Professional 7.8 (MapInfo Corporation, Troy, New York, USA). Sixty-two cells were selected randomly to receive a 1-km transect. Transect locations are shown in Figure 1b. Each transect's start coordinates were randomly located within each cell. End coordinates were obtained from a randomly selected compass direction 1-km away from the start coordinates, uploaded on to a handheld GPS (Garmin 60) using Garmin MapSource 6.11.6 (Garmin Ltd. Olathe, USA), and located on foot.

Elephant dung density as an index of elephant distribution and habitat use

We used elephant dung density to assess elephant habitat use. Elephant dung density has been used as an index of elephant distribution and habitat use for both African forest elephant (*Loxodonta africana cyclotis*) (Barnes *et al.* 1991) and Asian elephant (Varma 2008). Line transects as described by Buckland *et al.* (2004) were used to estimate elephant dung densities and the data were analysed using the program DISTANCE 6.0 (Thomas *et al.* 2010). The perpendicular distance of all dung piles sighted from the line transect was measured using a standard 30-m measuring tape. Estimates of dung density were obtained from the perpendicular distances (Barnes & Jensen 1987).

Predictors of variation in elephant dung density

We reviewed the literature on elephant habitat use to derive a set of likely environmental variables that have previously been suggested to influence elephant distribution and density in Mudumalai (Daniel *et al.* 1987, Desai & Baskaran 1996, Sivaganesan 1991). To estimate *L. camara* invasion intensity, the girth of all *L. camara* stems were measured at ground level within 10 × 1-m plots defined every 100 m to sample at 11 plots along each transect. We used 1-cm categories. The average *L. camara* girth for each plot was averaged over all 11 plots to give a *L. camara* invasion intensity for each transect.

Grass cover (forage) and canopy cover (shade) were estimated in each plot. A visual estimate of percentage grass cover to the nearest 5% cover was recorded in the plots. The average of all values of grass cover for each plot was used as the estimate for each transect. Canopy cover along each 1-km transect was estimated every 100 m using a 24 × 16-cm convex mirror divided into 24 equal cells (6 × 4 cells) and placed on the ground to reflect the canopy. If a cell reflected > 50% canopy cover then it was counted as having canopy cover. If a cell reflected < 50% canopy cover, it was ignored. Percentage canopy cover at the point was estimated as an index of shade. The average

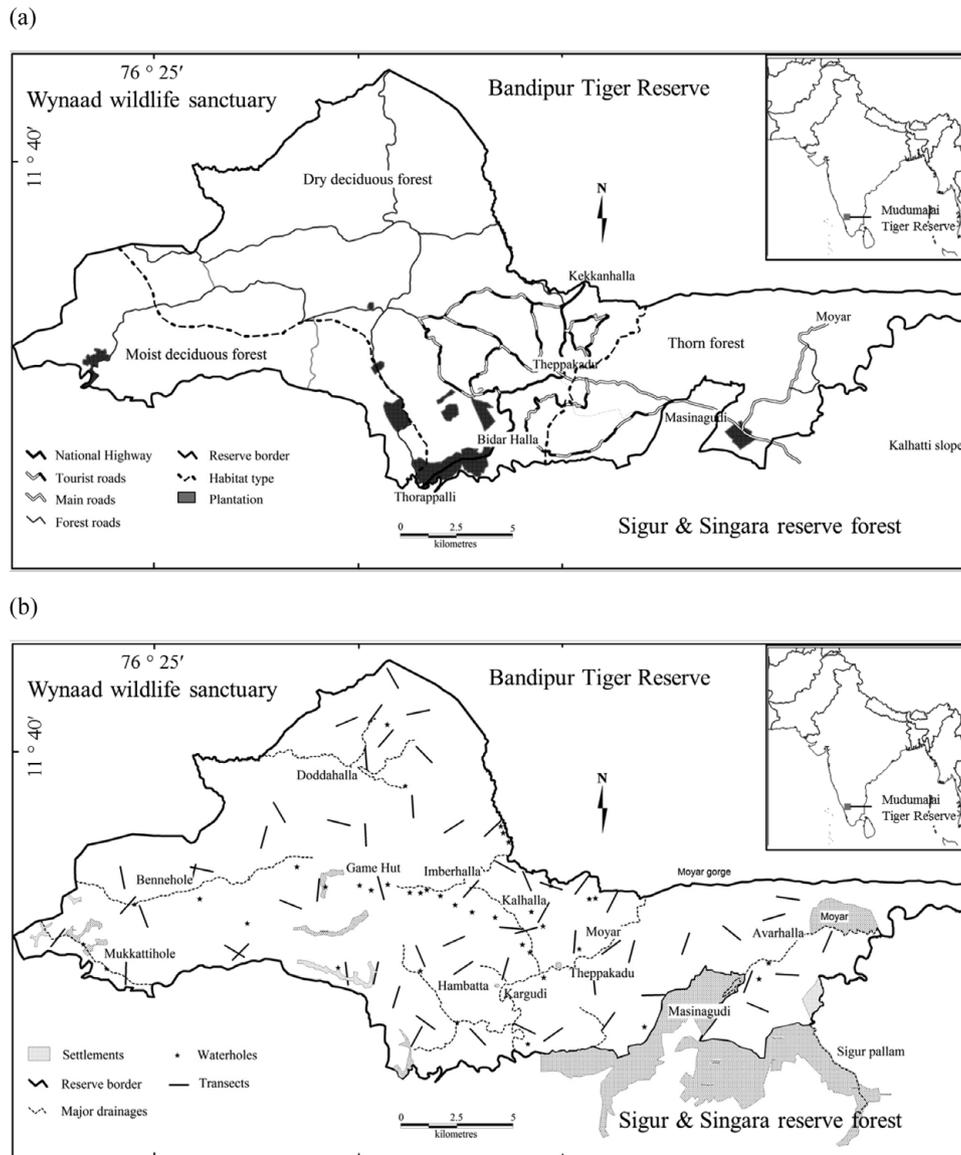


Figure 1. Mudumalai Tiger Reserve and its location in India showing the reserve with the major habitats: moist deciduous, dry deciduous and thorn forest delimited by a line. The road network distinguished as National Highway, main road for public use, tourist roads where only forest department vehicles are permitted, and forest roads are shown. Plantations are shown as black dotted patches (a); layout of the 62 transects across Mudumalai. Major drainages are shown by dotted lines. The location of water holes is shown by stars. Settlements are shaded in grey (b).

value of canopy cover from all points along each transect was used as the estimate in the analysis.

The size and thus potential impact of settlements on elephant varied throughout Mudumalai. We therefore had three categories for the variable settlement: (1) if a transect fell more than 2 km from a minor settlement; (2) if a transect fell within 2 km from a minor settlement; and (3) if a transect fell within 2 km of a major settlement. Similarly, the potential impact of roads on elephant differed, with the greatest impact from the National Highway passing through Mudumalai. This highway was considered to have the highest impact because vehicular traffic that included goods,

passenger, tourist and private vehicles used the National Highway. The impact of roads were categorized as follows: (1) Kekkanhalla to Theppakadu and Theppakadu to Masinagudi; (2) Theppakadu to Bidderhalla; (3) Bidderhalla to Thorappalli; (4) Kalhatti slopes; (5) forest roads within the tourist zones in Mudumalai where only Forest Department vehicles are allowed; (6) all other roads within Mudumalai (Figure 1a). As the Moyar river runs parallel to the National Highway between Theppakadu and Bidderhalla, this part of Mudumalai was considered to have high impact on elephant because elephants regularly crossed the roads to drink from the river but were often stranded because of vehicular traffic. Within

Mudumalai, smaller forest roads that were used only by the forest department's tourist vehicles had less impact while roads beyond the tourism zone were considered to have minimal impact on elephant distribution and habitat use.

To measure water availability, linear distances between the midpoint of each transect and the closest waterhole were measured from 1:50 000 topographic maps using MapInfo Professional 7.8 (MapInfo Corporation, Troy, New York, USA) (Figure 1b). The influence of anthropogenic fire on each transect was assessed by calculating the time since the last burn occurred in the area sampled. Thus, a transect sampled in 2009 that had burned in the year 2008 was given a value of one indicating that it was at least 1 y since it last burned. If more than 50% of a transect length burned in a particular year, it was considered as burned that year. Data on fire burns between 2003 and 2008 were obtained from the Tamil Nadu Forest Department Management Plan (Srivastava 2009), as monitored by Centre for Ecological Sciences, Indian Institute of Science, Bangalore. One of us (GW) recorded whether the transect burned in the year of sampling. Transects were overlaid on these fire maps and assessed.

Statistical methods

DISTANCE program 6.0 (Thomas *et al.* 2010) was used to analyse estimates of elephant dung density along the transects. Data filters and models were performed at various levels of truncation to improve the model fit (Buckland *et al.* 2004). The fit of the best possible model was determined by using Akaike's Information Criterion (AIC) (Akaike 1973) values that were generated by the program as well as by visually judging the fit of the proposed model to the observed distance data close to the line transect.

Dung density was first examined for normality. The skewness and kurtosis were both within the limits of normality and so normal theory models were used. Throughout, we used the Generalized Linear Model approach (McCullagh & Nelder 1983), with normally distributed errors and the identity link, as this allowed comparable analyses between the General Linear Models and the information-theoretic (I–T) approach. To investigate multicollinearity between the predictor variables, a correlation analysis was conducted. The largest correlation across habitats was between grass cover and *L. camara*, and was -0.360 . We therefore concluded that multicollinearity was not a significant issue with these data, and the parameter estimates and P-values were valid. SPSS Statistics, release version 20.0 (IBM SPSS Inc., Chicago, IL, USA) was used to analyse the data.

Our first hypothesis tested whether the addition of *L. camara* to other environmental variables significantly predicted habitat use by elephant across habitats in Mudumalai. We used a Generalized Linear Model (with a normal distribution and identity link) to predict elephant usage (based on dung density estimates).

Our second hypothesis tested whether models containing *L. camara* better explained elephant habitat use across habitats. We used an I–T approach (Burnham & Anderson 2002) to develop the best model using available environmental (predictor) variables to explain elephant habitat use based on dung density estimates across Mudumalai. The I–T methods provide formal measures of the strength of evidence for alternative models, given the data (Hegyí & Garamszegi 2011). The I–T approach allows us to rank and weigh multiple competing models. We used a second-order Akaike's Information Criterion (AIC_c) as our I–T statistic because models were large (i.e. with up to 51 explanatory variables; Burnham & Anderson 2002). Models with $\Delta AIC_c \leq 2$ were considered to have substantial support from the data and models with $\Delta AIC_c > 12$ to have no support or be implausible (Burnham & Anderson 2002).

Our third hypothesis examined whether *L. camara* along with significant environmental variables predicted habitat use by elephant within the dry deciduous forest. A Generalized Linear Model (with a normal distribution and identity link) was used to predict elephant usage (based on dung density estimates) using the main effect of *L. camara* and significant environmental variables from the models and tested for overall significance.

RESULTS

Elephant dung density and *Lantana camara*

The number of elephant dung piles counted along 1-km line transects varied between zero and 32 dung piles in Mudumalai. Estimates of dung pile density based on the DISTANCE algorithm ranged from zero to 6650 dung piles km^{-2} with an interquartile range of 2265 dung piles km^{-2} . *Lantana camara* density per $10 \times 1\text{-m}$ plot varied from 0 to 39 individuals and average stem girth per $10 \times 1\text{-m}$ varied from 0.14 cm to 11.8 cm. There was a significant negative correlation between elephant distribution and *L. camara* at the landscape level ($r = -0.253$, $n = 62$, $P = 0.047$, Figure 2a).

Influence of *Lantana camara* on elephant habitat use at the landscape level in Mudumalai

We first fitted a model (Model 1) which included habitat, impact of settlement, impact of roads, canopy cover, grass

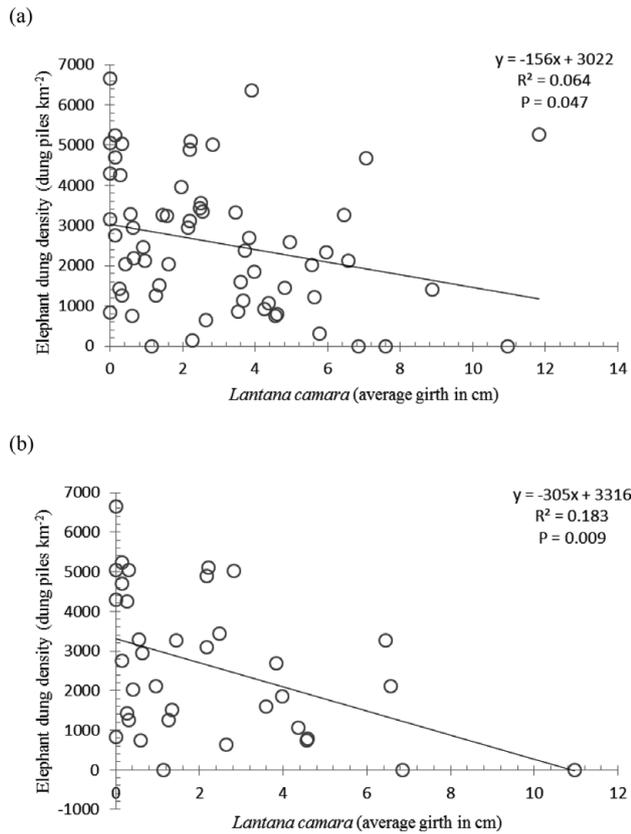


Figure 2. The relationship between elephant dung density (dung piles km^{-2}) and *Lantana camara* across habitats (a) and in the dry deciduous forest (b) in Mudumalai Tiger Reserve.

cover, fire, distance to water, and second-order interactions between factors. This model overall did not significantly predict dung density ($\chi^2 = 28.6$, $df = 23$, $R^2 = 0.37$, $P = 0.191$, $AIC_c = 1440.56$). Impact of settlement ($P = 0.007$), impact of roads ($P = 0.035$) and habitat

by impact of settlement interaction ($P = 0.030$) were individually significant.

To examine our first hypothesis that the addition of *L. camara* significantly predicted dung density across all habitats, we added *L. camara* to Model 1, to give Model 2. This model, overall did not significantly predict dung density ($\chi^2 = 30.4$, $df = 24$, $R^2 = 0.39$, $P = 0.172$, $AIC_c = 1582.19$). Only impact of settlement ($P = 0.003$) and habitat by impact of settlement interaction ($P = 0.024$) were significant predictors of dung density.

Model 3 included habitat, impact of settlements, impact of roads, canopy cover, grass cover, fire, water, *L. camara* and its interaction with habitat (DDF by *L. camara*, MDF by *L. camara*). Model 3 did not significantly predict dung density ($\chi^2 = 21$, $df = 16$, $R^2 = 0.81$, $P = 0.178$, $AIC_c = 1130.02$). The only significant predictor in the model was DDF by *L. camara* interaction ($P = 0.038$, Table 1).

Lantana camara was significantly related to dung density ($\chi^2 = 4.1$, $df = 1$, $R^2 = 0.06$, $P = 0.039$), but when other variables were accounted for, the relationship between *L. camara* and dung density was only through habitat. In particular, *L. camara* had a strong negative relationship with dung density in the DDF ($P < 0.05$).

Comparison of models using the information-theoretic approach

Our second hypothesis tested whether models containing *L. camara* better explained elephant habitat use across habitats. We used the I-T approach to develop the most informative model. Model selection using the I-T approach indicated that the model explaining elephant habitat use based on elephant dung-density estimates was Model 3 that included habitat, impact of settlement, impact of road, canopy cover, grass cover, fire, distance to water, *L. camara* and its interaction with DDF

Table 1. Model 3 with *Lantana camara* on its own, the interaction terms of *L. camara* with the dry deciduous (DDF) and moist deciduous forest (MDF) and environmental variables predicting elephant dung density estimates across habitats in Mudumalai Tiger Reserve. The beta coefficients, SE, Wald Chi-Square and levels of significance with main effects of environmental variables measured are shown. Factors (habitat, impact of settlements and roads) are entered as multiple dummy variables. For categorical factors with greater than two levels, the ranges of beta coefficients and SE are given.

Source	B	SE	Type III		
			Wald Chi-Square	df	P
(Intercept)	-314	1740	4.9	1	0.027
Habitat	2355-3174	1850-1997	2.5	2	0.282
Impact of settlements	1444-1491	806-897	3.6	2	0.162
Impact of roads	-876 to 749	617-1201	4.8	5	0.443
Canopy cover	-14	18	0.7	1	0.419
Grass cover	4	10	0.2	1	0.695
Fire	106	140	0.6	1	0.453
Water	50	326	0.0	1	0.878
<i>Lantana camara</i>	266	192	1.9	1	0.165
MDF \times <i>Lantana camara</i>	-262	343	0.6	1	0.445
DDF \times <i>Lantana camara</i>	-518	250	4.3	1	0.038

Table 2. Three statistical models for elephant habitat use in Mudumalai Tiger Reserve between January and May 2009 and November 2009 and May 2010. The models are in descending order based on the second-order Akaike's Information Criterion (AIC_c). The model consisting of *Lantana camara* and its interaction with habitat along with other environmental variables was the leading model and only model to receive substantial support. *K* is the number of parameters in each model which includes the intercept.

Model	Predictor variables	K	AIC _c	Δ AIC _c	ω
3	Habitat, impact of settlement, impact of roads, canopy cover, grass cover, fire, distance to water, <i>Lantana camara</i> , MDF × <i>Lantana camara</i> , DDF × <i>Lantana camara</i>	20	1130.02	0.00	1.000
1	Habitat, impact of settlement, impact of roads, canopy cover, grass cover, fire, distance to water, habitat × settlement, habitat × roads, settlement × roads	48	1440.56	310.54	0.000
2	Habitat, impact of settlement, impact of roads, canopy cover, grass cover, fire, distance to water, habitat × settlement, habitat × roads, settlement × roads, <i>Lantana camara</i>	51	1582.19	452.17	0.000

($\Delta AIC_c \leq 2$; $\omega_i = 1.000$). This was the only model to receive any support. The two other models (Model 1 and Model 2) received no support and were implausible (i.e. $\Delta AIC_c > 10$, Table 2).

Influence of *Lantana camara* on elephant habitat use within the dry deciduous forest in Mudumalai

Our third hypothesis tested whether *L. camara* significantly influenced habitat use by elephant at a lower scale, within habitat. We analysed the data for the DDF separately given that the interaction term DDF by *L. camara* was significant in Model 3.

The model included impact of settlement, impact of road and *L. camara* which significantly predicted dung density in the DDF ($\chi^2 = 8.6$, $df = 3$, $P = 0.04$). *Lantana camara* was the only significant predictor ($\chi^2 = 4.6$, $df = 1$, $P = 0.03$, $B = -300 \pm 140$). There was a significant negative correlation between elephant distribution and *L. camara* in the DDF ($r = -0.427$, $n = 36$, $P = 0.009$, Figure 2b). There was also a significant negative correlation between per cent grass cover and *L. camara* ($r = -0.565$, $n = 36$, $P < 0.05$) in the DDF.

DISCUSSION

Influence of *Lantana camara* on elephant habitat use at the landscape level in Mudumalai

Our first hypothesis determined whether the addition of *L. camara* had an influence on elephant habitat use in Mudumalai. The results of our study found no evidence that the addition of *L. camara* did influence elephant habitat use at the landscape level, however, we did find support for the hypothesis that *L. camara* negatively influenced elephant habitat use within the DDF at a lower spatial scale.

Our study shows that habitat and the impact of settlements are associated with elephant habitat use in Mudumalai and appear to have substantially more of an influence on elephant distribution and habitat use at

the landscape level than *L. camara*. Although elephants are known to use all habitats throughout the year in MTR, their densities vary across habitats (Sivaganesan 1991). Movement across different habitats is governed by seasons and home ranges (Baskaran 1998, Sukumar 1989). Elephants have large home ranges in excess of 550 km² in the study area (Baskaran *et al.* 1995) and hence they move across multiple habitats based on movement patterns established by individual clans and bulls. So habitat-use at the landscape level is largely governed by seasonal changes in resource availability. Additional problems in detecting the influence of *L. camara* on elephant distribution at the landscape level originate because elephants may have used *L. camara* areas just for resting or to pass through while looking for suitable feeding grounds and feeding on available grass patches around *L. camara* and during this time may have defecated. Such habitat use would make the influence of *L. camara* less visible, especially at the landscape level.

Invasive weeds such as *L. camara* on the other hand, would potentially influence elephant habitat use at lower scales covering smaller patches within a given habitat. *Lantana camara* patches are significantly smaller than settlements. Additionally, *L. camara* patches are not uniformly distributed and hence the influence of *L. camara* for different transects could vary, unlike settlements which are avoided by elephants (Desai & Baskaran 1996) and their impact therefore is uniform for a given distance from the settlement. However, *L. camara* has an influence on a much smaller spatial scale which represents smaller areas within a habitat. This is clearly evident as the interaction term, DDF by *L. camara*, in Model 3 is statistically significant. Hence, analysing the influence of *L. camara* within individual habitats is more appropriate, as on a larger spatial scale, variables such as habitat and settlements confound the results.

Comparison of models using the information-theoretic approach

Our second hypothesis tested whether models containing *L. camara* better explained elephant habitat use across

habitats by using the I–T approach to compare models explaining elephant habitat use. The addition of *L. camara* to the model that included habitat, impact of settlement, impact of roads, canopy cover, grass cover, fire, distance to water, and second-order interactions between factors was not supported nor was the model without *L. camara*. The only model that received strong support was Model 3 that included habitat, impact of settlements, impact of roads, canopy cover, grass cover, fire, water, *L. camara* and its interaction with habitat (DDF by *L. camara*, MDF by *L. camara*). The only significant predictor in this model was the interaction term, *L. camara* by DDF, indicating that *L. camara* may in fact have a role at a different spatial scale.

Influence of *Lantana camara* within the dry deciduous forest of Mudumalai

Our third hypothesis determined whether *L. camara* significantly influenced habitat use by elephant within the DDF, since the interaction between *L. camara* and DDF was significant. Given that habitat and impact of settlements may confound the results at larger spatial scales, one would therefore expect that an analysis on a smaller spatial scale, within individual habitats, would show that *L. camara* has an influence on elephant distribution; especially within habitats. Our results indicated a significant influence of *L. camara* in the DDF. These results are supported by other empirical studies that have shown a negative impact of invasive weeds on ungulates (Hein & Miller 1992, Trammell & Butler 1995). Typically the elephant is more dependent on grass in the DDF and the thorn forest (TF) than in the moist deciduous forest (MDF) (Baskaran 1998, Sivaganesan & Johnsingh 1995). However, the negative correlation between *L. camara* and grass cover implies that the elephant may be avoiding areas where there is more *L. camara* due to the loss of grass. The negative correlation between elephant distribution and *L. camara* was statistically significant in the DDF but was not statistically significant in the TF and MDF. Grass is not a major food source in MDF but is a dominant food in both DDF and TF (Baskaran *et al.* 2010b). Thus, analysis at the landscape level results in the major predictors for movement at larger scales (habitat and impact of settlements) to be detected but *L. camara* drives habitat selection at a far smaller scale of a few ha to a few km² and hence its influence is more easily detected when within-habitat assessment is performed.

Implications for conservation

Invasive weeds such as *L. camara* influence elephant at different spatial scales and have different influences in

different habitats. Our study finds no evidence that *L. camara* has affected elephant habitat use at the larger spatial scale of a landscape, but we did find support for the hypothesis that *L. camara* does have an influence at the smaller spatial scale of a single habitat. Since *L. camara* patches are not uniformly distributed and elephants do not eat *L. camara*, they are forced to selectively graze within and around *L. camara* patches (Wilson, unpubl. data). The primary influence *L. camara* has on the elephant habitat is the reduction of grass cover. This is clearly seen from the negative correlation *L. camara* has with grass in the dry deciduous forest. The presence and spread of *L. camara* can therefore be considered as being adverse to elephants and other grazing herbivores. Selective grazing can reduce available forage and possibly favour the spread of invasive weeds (Lym & Kirby 1987, Vavra *et al.* 2007) such as *L. camara*. This selective grazing in turn could reduce the overall carrying capacity of elephants in Mudumalai. In North Dakota, leafy spurge (*Euphorbia esula*)-infested areas represented an annual herbage loss of 35% (Lym & Kirby 1987). A similar loss to grass and other native tree species may be occurring within Mudumalai. Lym & Kirby (1987) reported an increased use of sites by cattle not infested by leafy spurge, which decreased preferred herbage and decreased species diversity. An increased use of non-infested sites would reduce the carrying capacity as a result of over-grazing and over-browsing of sites free of infestations (Trammell & Butler 1995). Managers should consider removal of weeds particularly in the DDF, and thereby increase forage production in order to maintain habitat suitability for elephants and other grazing herbivores.

As *L. camara* densities vary in different vegetation (Wilson, unpubl. data) and the evidence shows that *L. camara* influences habitat use at different spatial scales, it would be important that further studies at different spatial scales within each habitat be conducted to assess the true impact of *L. camara* on elephant and their habitat use. Our study indicates that the effect of *L. camara* is not uniform, and thus *L. camara* management could focus on specific habitats enabling managers to use their limited resources where they are most required.

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