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Foraging Relationships Between Elephants and *Lantana camara* Invasion in Mudumalai Tiger Reserve, India

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ABSTRACT

Lantana camara is a widespread exotic invasive species in India, capable of dominating and displacing native forage species. We investigated whether *L. camara* was associated with variation in elephant foraging behavior in Mudumalai Tiger Reserve, India. The behavioral responses of elephants to *L. camara* were assessed from feeding and stepping rates. Elephants were never observed to feed on *L. camara,* but rather fed on grass and browse present within and around *L. camara* patches. A multiple regression analysis showed that feeding rates were negatively associated with *L. camara* invasion ($F_{1,\ 55} = 4.26$, $R^2 = 0.07$), but not stepping rates. Instead, grass cover and browse density were associated with stepping rates ($F_{2,\ 55} = 11.16$, $R^2 = 0.30$). Path analysis indicated that the total effect of *L. camara* on feeding rates was 11 percent ($\beta = -0.24$) less than the direct negative association ($\beta = -0.27$) owing to a positive indirect association of *L. camara* with feeding rates through grass cover and browse density ($\beta = 0.03$), while stepping rates were negatively associated with grass cover ($\beta = -0.39$) and positively associated with browse density ($\beta = 0.38$). Our results indicate that *L. camara* appears capable of modifying feeding rates of elephants, likely through a loss of grass areas due to *L. camara* invasion. Experimental work is needed to test for causal relationships among the variables we measured, to enhance our understanding of how invasive weeds modify elephant behavior.

Key words: dry deciduous forest; elephant; feeding rates; path analysis; stepping rates; weed invasion.

Foraging decisions are guided by behavioral predisposition and inherited skills that are refined through experience and accumulation of knowledge (Launchbaugh & Howery 2005). According to the rate maximizing foraging theory, animals make choices that maximize the net rate of energy intake while foraging (MacArthur & Pianka 1966, Nagarajan *et al.* 2002). To meet their metabolic requirements, herbivores must make these food-choice decisions while maintaining an adequate nutrient intake (Owen-Smith 1979). However, unpalatable invasive weeds may render some areas unsuitable to herbivores through reduced forage, limiting food resources to fewer patches (Atwater *et al.* 2011), especially if the weed is not eaten. In particular, invasive plants might reduce food availability for large mammalian herbivores whose metabolisms need large volumes of food daily (Owen-Smith 1988, Dumonceaux 2006). In some cases, substantially lower leaf herbivory was experienced by highly invasive exotic plants when compared with non-invasive exotics (Cappuccino & Carpenter 2005). Weed invasion, therefore, is expected to modify herbivore feeding behavior through an increase in unpalatable or low nutritional value food species.

Biological invasions are characterized by the spread of exotic species in areas newly inhabited by the species (Hengeveld 1988). Invasive plants have been shown to modify habitat use by a wide range of wild and domestic herbivores (Hein & Miller 1992, Trammell & Butler 1995), alter abundances of birds, reptiles (Aravind *et al.* 2010, Kutt & Fisher 2011), and even grizzly bears (*Ursus arctos horribilis*) (Reinhart *et al.* 2001). Invasive plants might even have a toxic effect on herbivores (Sharma *et al.* 1981). Furthermore, invasive plants might also have a direct negative effect on native herbivore food plants. Depending on the interactions among competitors and consumers, indirect interactions between invasive and native plants may also decrease the direct negative effects of invasive plants on native plants because of indirect positive effects such as reduced competition from other native plants and lower levels of herbivory (Atwater *et al.* 2011). Thus, investigating direct and indirect pathways may help understand the role of invasive weeds and their interaction with native plants and consumers.

It is particularly challenging to demonstrate the mechanism of impact of invasive weeds on wild megaherbivores such as elephant, where no direct outcomes can be easily measured. In comparison, in the livestock industry, the impact of poisonous range weeds has been shown to have an indirect impact on cattle and sheep in terms of reduced reproduction, and lower milk quality and wool production (Frandsen & Boe 1991). No such productivity estimates are easily obtainable for wild animal populations. One way to examine the mechanism of influence of invasive weeds is through studying herbivore behavior (for example, feeding and stepping rates while feeding) in habitat that varies in levels of weed invasion.

The Asian elephant (*Elephas maximus*) has been known to have a major effect on ecosystem functioning and vegetation dynamics and structure (Sukumar 1989, Sivaganesan &

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Sathyanarayana 1995). Elephants feed on large quantities of vegetation on a daily basis. They are able to switch between grass and browse depending on season and availability (Sukumar 1989, Baskaran 1998). In terms of its biomass, the elephant is a major contributor to total large herbivore biomass (Sukumar 1989). It is also recognized as a flagship species of conservation interest (Blake & Hedges 2004).

A number of studies have been conducted on the ecology of elephants in Mudumalai Tiger Reserve (hereafter Mudumalai) in southern India, including ranging, habitat use, and foraging behavior (Sivaganesan 1991, Baskaran 1998). While these studies have drawn attention to the proliferation of exotic weeds such as *Lantana camara*, *Chromolaena odorata*, *Ageratum conyzoides*, and *Parthenium hysterophorus*, a recent study by Wilson *et al.* (2013) showed that there were negative impacts of the invasive weed on elephants in Mudumalai. Elephants have been observed to spend between 60 and 74 percent of their day foraging on grass (graminoids) and browse (dicotyledons) in Mudumalai depending on season and habitat (Sivaganesan & Johnsingh 1995, Baskaran *et al.* 2010a). The basic classification in terms of plant species that are eaten is the graminoid:dicotyledon proportions (including non-graminaceous monocots with dicots) (Owen-Smith 1988). Grass has been shown to form a major component of elephant diet (85%), whereas browse accounted for about 15 percent of elephant forage in this reserve (Baskaran *et al.* 2010a). Thus, elephant in this reserve are predominantly grazers. If the proliferation of weeds did influence elephant by either occupying space or displacing native forage species (grass and browse), it is possible that elephants may modify their foraging behavior depending on the level of invasion.

Despite its large size, the elephant habitat is exposed to severe threats in the form of weed proliferation and biotic pressure from the surrounding human population. Weeds like *Lantana camara*, *Chromolaena odorata*, *Ageratum conyzoides*, and *Parthenium hysterophorus* have spread extensively, visibly reducing grass cover and potentially reducing regeneration and recruitment of trees and shrub species. An increase in *L. camara* an alien invasive weed in Mudumalai and the surrounding regions has caused concern about its effects on native floral communities and in turn on the herbivore community (Prasad 2012, Ramaswami & Sukumar 2013). A shrub native to the American tropics, *L. camara* was introduced to India as an ornamental plant in the early 1800s and its presence has been recorded from the central Himalayas in the north to southern India (Kannan *et al.* 2012). The earliest record of the presence of *L. camara* in the Nilgiris in southern India was in 1880 (Beddome 1880). However, it was not until 1921 that *L. camara* was recognized as a troublesome weed, and eradication of *L. camara* began in 1924 in Benne and Mudumalai blocks of Mudumalai (Troupe 1921). By 1941, *L. camara* was described as being a problem and was spreading rapidly in the dry deciduous forest and teak plantations of Mudumalai (Ranganathan 1941).

Despite *L. camara* being known to have negative impacts on native biota (Sharma & Raghubanshi 2007, Prasad 2010), some studies have shown that native floral species seemed unaffected by the presence of *L. camara* (Ramaswami & Sukumar 2013), whereas other studies have in fact shown an increase in certain bird species (Aravind *et al.* 2010). Nevertheless, given the significant negative association of *L. camara* with elephant habitat use in the dry deciduous forest of Mudumalai (Wilson *et al.* 2013), we tested the hypotheses that variation in elephant foraging behavior is associated with variation in *L. camara* invasion in the dry deciduous forest. Elephant foraging behavior was examined from feeding and stepping rates while feeding at different levels of *L. camara* invasion.

METHODS

STUDY SITE AND ELEPHANT POPULATION.—Mudumalai Tiger Reserve (11°32′–11°42′ N, 76°20′–76°45′ E) is located at the tri-junction of the 5500-km^2 Nilgiri Biosphere Reserve, in the state of Tamil Nadu, Southern India. Bandipur Tiger Reserve lies to the north, and Wynaad Wildlife Sanctuary lies to the west and northwest of Mudumalai. Singara and Sigur Reserve forests form the southern and eastern boundaries, respectively (Fig. S1). The wild elephant population in Mudumalai was estimated at 768 (95% lower and upper confidence interval = 536–1001) (Baskaran *et al.* 2010b). Mudumalai has been classified into three major habitats based on vegetation types (Champion & Seth 1968). For this study, only the dry deciduous forest ($\approx$ 195 km^2) was chosen for a finer spatial scale study. A focus on the dry deciduous forest allowed increased replication and sampling.

ELEPHANT BEHAVIORAL OBSERVATIONS (FOCAL ANIMAL SAMPLING).—Wild elephants were observed to examine the behavioral response of elephants to *L. camara* invasion while foraging. Field observations and measurements were conducted between January and May 2009, and November 2009 and May 2010. Observations of sub-adult and adult elephants were made during daylight between 0600 and 1800 h. These elephants were typically observed in groups. Elephants were located from the road and approached on foot, downwind, to minimize disturbance from observers. The first individual seen, or the closest elephant at the beginning of data collection, was selected from the herd, and focal animal sampling method (Altmann 1974) was adopted to sample its feeding. Locations of the feeding sites were taken where the sampling observation of an elephant began (Fig. S1) using a GPS (Garmin 60).

Observation periods varied from 10 min to 5 h depending on the length of time the elephant was visible and normal feeding behavior was observed (*i.e.*, no disturbance from people, vehicles, or other elephant groups). Viewing distance ranged from 10 m to approximately 50 m. Standard 7′ × 50″ binoculars were used for observations and care was taken to minimize disturbance to the group. When the focal elephant was not visible during the observation period, recording stopped and the interval was noted, so that these minutes could be deducted from the sampling period. Recording of feeding behavior (trunksful and steps, see below) resumed when the same focal elephant reappeared. If a focal elephant remained out of view for more than 5 min, the next closest elephant seen at the time of observation was chosen for another sample, if changing the observer location did not address the situation. In this way, a previously sampled individual was never re-sampled. Fifty-seven individual elephants were sampled for a total of 64.3 h.

To assess the behavioral response of elephant to *L. camara* invasion, we used feeding rates derived from observations of the number of trunksful/min (Sivaganesan 1991, Baskaran 1998). Feeding rates, defined as the number of trunks of grass or browse that the focal elephant gathered with its trunk and put into its mouth, were recorded every minute until the elephant was no longer visible. Browse and major grass species that were eaten were identified and recorded.

To further assess the behavioral association between elephant and *L. camara* invasion, we also assessed stepping rates while feeding, derived from the number of steps/min during the period of observation. One step was defined as the movement of one back foot from one place to another followed by the second foot, without placing the first foot back where it came from.

SAMPLING ENVIRONMENTAL COVARIATES.—The sites' characteristics (environmental covariates) between the start and end points of each sampling observation were measured from straight line transects. Transect lengths varied from 50 m to 500 m depending on the distance the elephant moved during the sampling period (Table S1). Environmental covariates of the feeding sites, measured from 10 × 1 m plots, spaced 50 m apart along each transect were *L. camara* invasion, canopy cover, browse density, and percentage grass cover.

To estimate *L. camara* invasion, an estimate of the age of the stand defined by stem girth of *L. camara* plants at ground level was measured and recorded in 1 cm categories. An average girth for each plot was obtained. The average *L. camara* girth for each plot was averaged over all plots along each transect, to give an estimate of *L. camara* invasion for each transect. The number of plots within each transect varied, depending on the distance the elephant moved. Browse density (shrubs and saplings measuring 10–150 cm in height) was derived from the same plots measuring 10 × 1 m along each transect. A visual estimate of percentage grass cover to the nearest 5 percent cover was recorded in each plot and was averaged over all plots as the estimate for each transect.

Canopy cover along each transect was estimated every 50 m using a 24 × 16 cm convex mirror divided into 24 equal squares (6 × 4 cells) and placed on the ground to reflect the canopy cover. A cell reflecting greater than 50 percent canopy cover was counted as having canopy cover, while a cell reflecting less than 50 percent canopy cover was ignored. The percentage canopy cover that was estimated at the point served an index of shade. The average value of canopy cover from all points within each transect was used as the estimate in the analysis.

DATA ANALYSIS.—Linearity was examined by plotting the relationship between the response variable (feeding and stepping rates) and each predictor variable (environmental covariates) using Minitab's lowess plot (smoothening parameter 0.5), Minitab 15 (Minitab, State College, Pennsylvania, U.S.A.). To investigate multicollinearity between the environmental covariates, a correlation analysis was conducted before using stepwise multiple regressions to assess the relationships between the response variable and predictor variables, thereby providing valid parameter estimates and *P* values. Feeding and stepping rates were tested against measured environmental covariates (*L. camara* invasion, percentage canopy cover, percentage grass cover, and browse density) using stepwise multiple regression. The data were analyzed using SPSS Statistics, 20.0 (IBM SPSS Inc., Chicago, Illinois, U.S.A.). Prior to analysis, these data were normalized using $\log_{10}$ transformations on feeding and stepping rates and browse density and arcsine-square root transformations on percentage grass cover and canopy cover.

To examine for relative direct and indirect effects of environmental covariates on feeding and stepping rates, we used a path analysis (Wright 1968). The process involves an analysis among a set of variables for a hypothesized causal structure or path model. A path analysis assumes linear relationships between variables with normal distributions. All variables were transformed to conform to this assumption, and analyses were conducted using AMOS 19.0 (Arbuckle 2010). Path analysis tests whether the total observed covariance structure is reflected in the covariance structure of a subset of relationships among a group of variables. If the covariance structure of the path diagram does not differ from the total observed covariance structure, then a statistically insignificant result will be obtained, indicating a good fit to the data (Arbuckle 2010). A hypothesized subset of relationships between variables (path diagrams), one for feeding rates and one for stepping rates, were constructed (Fig. 1). In

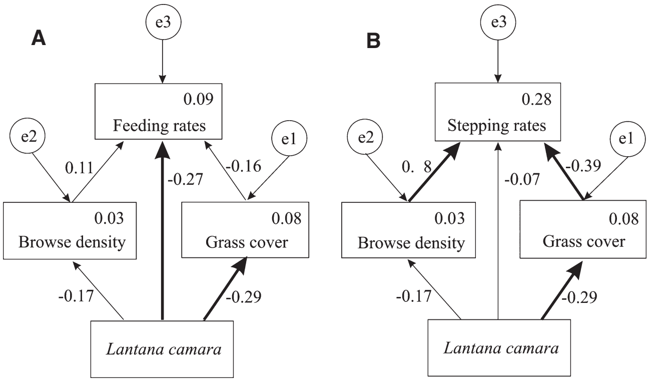

FIGURE 1. Path diagrams and path coefficients of (A) feeding rates and (B) stepping rates. The path diagram predicted that (A) grass cover and browse density had a direct effect on feeding rates, while *Lantana camara* had direct and indirect effects on feeding rates through grass cover and browse density; (B) grass cover and browse density had direct effects on stepping rates, while *Lantana camara* had direct and indirect effects on stepping rates through grass cover and browse density. Numbers in the boxes are R^2 values. Numbers near the arrows are path coefficients, and the circles labeled e1, e2, and e3 refer to error terms (N = 57). Significant relationships are shown by thick arrows. Path coefficients can be compared directly.

constructing the final model, we used logical inference rather than model selection.

RESULTS

The average girth of *L. camara* stems seen was 3.17 cm ± 0.31 (SE) per observation transect. Ten sampling transects out of 57 had no *L. camara* present. The maximum average *L. camara* girth was 9.50 cm, with an interquartile range of 3.06-cm diameter in areas where elephants were observed feeding. The mean canopy cover across transects was 37 ± 2.9 percent (SE), while the mean percentage grass cover was 61 ± 3.5 percent (SE). Mean browse density was 1.1 ± 0.1 percent (SE).

Fifty-seven elephants were observed over 64.3 h. Elephants were never observed to feed on *L. camara,* but were observed to eat grass species such as *Setaria intermedia, Digitaria* sp., and *Eragrostis* spp. growing on the edges of *L. camara* patches. These grass species appeared green (based on color) and moist even in dry season. Grass was a major component of elephant diet (88%, or 4399 of 4981 trunksful), while the remainder was browse (12% or 582 of 4981 trunksful), which included shrubs and saplings. The tall grass *Themeda cymbaria* contributed 76.2 percent (3352 of 4399 trunksful) of elephant diet, whereas *Pennisetum hohenackeri* found in the swamps, other tall grass species such as *Cymbopogon flexuosus*, *Imperata cylindrica,* and short grass species such as *T. triandra* and *S. intermedia* constituted the rest (23.8% or 1047 of 4399 trunksful).

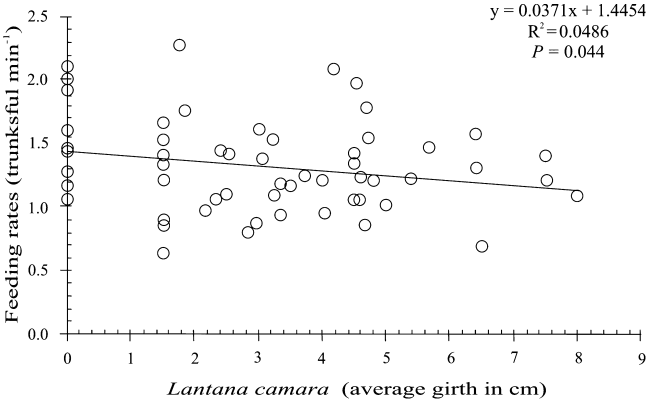

FIGURE 2. The relationship between *Lantana camara* and elephant feeding rates (trunksful/min) in the dry deciduous forest of Mudumalai.

FACTORS INFLUENCING FEEDING AND STEPPING RATES.—Stepwise multiple regression indicated that *L. camara* was the only variable that significantly predicted feeding rates ($F_{1,\ 55} = 4.26$, $P = 0.04$), although it explained only 7 percent of the variability in feeding rates. The relationship between *L. camara* and feeding rates was negative ($\beta = -0.27$, $t = -2.06$, $P = 0.04$; Fig. 2). Canopy cover, grass cover, and browse density were not associated with feeding rates ($P > 0.05$; Models 1–3, Table 1).

Stepwise multiple regression was also used to predict stepping rates of elephants while feeding in different levels of *L. camara* invasions. *Lantana camara* did not enter into the final model. The final model included grass cover and browse density ($F_{2,\ 55} = 11.16$, $P < 0.001$, $R^2 = 0.30$). These variables together significantly predicted stepping rates and explained 30 percent of the variability in stepping rates (Table 2). Stepping rates were negatively associated with grass cover ($\beta = -0.35$, $t = -3.05$, $P < 0.01$; Fig. 3A) and positively associated with browse density ($\beta = 0.39$, $t = 3.40$, $P < 0.01$; Fig. 3B; Table 2).

TABLE 1. *Stepwise multiple regression of factors used to predict feeding rates of elephant in Mudumalai Tiger Reserve (N = 57).* Lantana camara *was the only significant predictor of feeding rates of elephant.*

		Unstandardized coefficients		Standardized coefficients			95% confidence interval for B	
	Model	*β*	SE	*β*	*t*	*P*	Lower bound	Upper bound
1	(Constant)	0.20	0.08		2.52	0.015	0.04	0.37
	Canopy cover	0.04	0.07	0.08	0.54	0.592	−0.11	0.18
	Lantana camara	−0.06	0.03	−0.31	−2.11	0.040	−0.11	0.00
	Grass cover	−0.05	0.06	−0.13	−0.90	0.373	−0.17	0.06
	Browse density	0.01	0.02	0.08	0.60	0.553	−0.03	0.06
2	(Constant)	0.23	0.07		3.43	0.001	0.10	0.36
	Lantana camara	−0.05	0.03	−0.28	−2.06	0.044	−0.10	0.00
	Grass cover	−0.06	0.06	−0.14	−1.05	0.301	−0.17	0.05
	Browse density	0.02	0.02	0.11	0.80	0.428	−0.03	0.06
3	(Constant)	0.24	0.07		3.59	0.001	0.10	0.37
	Lantana camara	−0.06	0.03	−0.31	−2.28	0.027	−0.11	−0.01
	Grass cover	−0.06	0.06	−0.15	−1.15	0.257	−0.17	0.05
4	(Constant)	0.17	0.03		5.02	0.000	0.10	0.24
	Lantana camara	−0.05	0.02	−0.27	−2.06	0.044	−0.10	0.00

TABLE 2. *Factors used to predict stepping rates of elephant in Mudumalai Tiger Reserve using stepwise multiple regression (N = 57). Grass cover and browse density significantly predicted stepping rates of elephant.*

		Unstandardized coefficients		Standardized coefficients			95% confidence interval for B	
	Model	β	SE	β	t	P	Lower bound	Upper bound
1	(Constant)	0.49	0.12		3.98	0.000	0.25	0.74
	Canopy cover	−0.13	0.11	−0.15	−1.16	0.254	−0.35	0.09
	Lantana camara	−0.01	0.04	−0.02	−0.18	0.858	−0.09	0.08
	Grass cover	−0.29	0.09	−0.40	−3.27	0.002	−0.46	−0.11
	Browse density	0.11	0.03	0.42	3.40	0.001	0.05	0.18
2	(Constant)	0.49	0.12		4.18	0.000	0.25	0.72
	Canopy cover	−0.13	0.10	−0.16	−1.31	0.196	−0.34	0.07
	Grass cover	−0.28	0.09	−0.40	−3.32	0.002	−0.45	−0.11
	Browse density	0.12	0.03	0.43	3.63	0.001	0.05	0.18
3	(Constant)	0.37	0.08		4.82	0.000	0.22	0.53
	Grass cover	−0.25	0.08	−0.35	−3.05	0.004	−0.42	−0.09
	Browse density	0.11	0.03	0.39	3.40	0.001	0.04	0.17

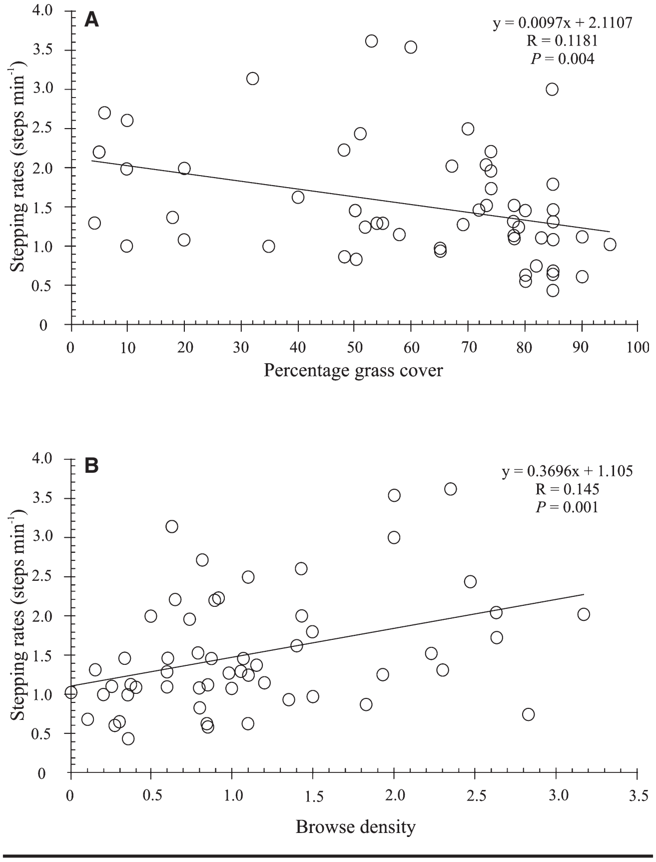

FIGURE 3. The relationship between elephant stepping rates (steps/min) and (A) percentage grass cover and (B) browse density.

In addition to the multiple regression analyses, we used a path analysis to estimate the relative importance of direct and indirect effects of *L. camara* and other potential variables on feeding and stepping rates. Given that elephants feed on grass and browse, the path analysis predicted that grass cover and browse density had a direct effect on feeding rates, while *L. camara* had both direct and indirect effects on feeding rates mediated by grass cover and browse density (Fig. 1A). The path analysis reflecting the relationship between stepping rates and environmental covariates predicted that grass cover and browse density had direct effects on stepping rates, while *L. camara*, which was our primary interest, had both direct and indirect effects on stepping rates mediated by grass cover and browse density (Fig. 1B).

Results from the path analyses for feeding rates (Fig. 1A) produced an insignificant likelihood ratio test ($\chi^2 = 0.77$, df = 1, $P = 0.38$), indicating a good fit to the data. As in the multiple regression analysis, the path analysis also suggested that feeding rates were negatively associated with *L. camara* ($\beta = -0.27$, $P = 0.05$). A significant negative relationship was seen between *L. camara* and grass cover ($r = -0.29$, $P = 0.03$) indicating that *L. camara* invasion was associated with reduced grass cover. The total effect of *L. camara* on feeding rates was −0.24 (0.05 + −0.02 = 0.03 + −0.27) (indirect effects through grass cover [−0.29 × −0.16 = 0.05] and browse density [−0.17 × 0.11 = −0.02] and direct effect [$\beta = -0.27$] on feeding rates). However, because *L. camara* also had a strong direct negative effect on grass cover ($\beta = -0.29$, $P = 0.02$) but no effect on browse density ($\beta = -0.17$, $P = 0.20$), the indirect effects of *L. camara* on feeding rates were positive. Consequently, the overall negative effect of *L. camara* on feeding rates was reduced by approximately 11 percent (from −0.27 to −0.24). Nevertheless, these variables (*L. camara*, grass cover, and browse density) together explained only 9 percent of the variation in feeding rates.

The path analyses on stepping rates (Fig. 1B) produced an insignificant likelihood ratio test ($\chi^2 = 0.76$, df = 1, $P = 0.38$), again indicating a good fit to the data. The analysis suggested that stepping rates were negatively associated with grass cover ($\beta = -0.39$, $P < 0.001$) and positively associated with browse density ($\beta = 0.38$, $P < 0.01$). In agreement with the multiple regression analysis, *L. camara* was not associated with browse density ($\beta = -0.17$, $P = 0.20$). The total effect of *L. camara* on stepping rates was -0.02 ($0.11 + -0.06 = 0.05 + -0.07$ [indirect effects through grass cover ($-0.29 \times -0.39 = 0.11$) and browse density ($-0.17 \times 0.38 = -0.06$) and direct effect ($\beta = -0.07$) on stepping rates]). Again, the indirect effects of *L. camara* on stepping rates were positive. As a result, the overall negative effects of *L. camara* on stepping rates were reduced by ≈ 71 percent (from -0.07 to -0.02). These variables together explained only 28 percent of the variation in stepping rate, which was less than the variation explained in the multiple regression (30%).

DISCUSSION

In this study, we examined the behavioral response of elephants to *L. camara* invasion while foraging in the dry deciduous forest of Mudumalai. Elephants were never observed to feed on *L. camara* and their feeding rates declined with an increase in *L. camara* invasion. Previous studies have shown that invasive weeds can influence foraging strategies of mammals either through reduction in forage production or reduced utilization of invaded habitats (for example, Hein & Miller 1992, Trammell & Butler 1995).

Path analysis indicated an overall negative association of *L. camara* with feeding rates. The direct negative association of *L. camara* with feeding rates was, however, reduced by 11 percent as a result of the indirect positive effect of *L. camara* on feeding rates through grass cover and browse. Most of the indirect positive effects of *L. camara* on feeding rates appeared to be due to reduced grass cover where *L. camara* was more prevalent. Elephants possibly increased their feeding rates due to reduced grass availability requiring them to gather more but smaller trunksful. Although indirect positive effects were observed, the overall effect was still negative indicating that *L. camara* reduced feeding rates in elephants because of the negative association of *L. camara* with grass that forms major elephant food. Thus, the positive indirect effects of *L. camara* through grass and browse as seen from the path analysis may be a consequence of elephant increasing their feeding rates because of lower grass biomass available, contrary to a site that is highly invaded and hence a direct negative association of feeding rates with *L. camara* where there is no grass. In our study, however, trunksful size was assumed to be constant, although in reality, trunksful size probably varied considerably. Any future assessment of feeding would ideally include measurement of the quantity of grass taken in each trunksful, so as to better correlate feeding rates with *L. camara* invasion.

The variation in feeding rates explained by *L. camara*, grass cover, and browse density was only 9 percent, which suggests that a number of unmeasured environmental covariates could explain more of the variation in feeding rates. For example, grass species composition, height of grass stand, texture, palatability, and nutrient content, none of which was measured in this study, have been shown to contribute to variation while feeding (Sivaganesan & Johnsingh 1995, Baskaran *et al.* 2010a). In addition, season and habitat type may indirectly influence the aforementioned environmental covariates.

The negative association of *L. camara* with feeding rates most likely resulted from the reduction and decline of grass, which is a major elephant food source (88%). Invasive alien plants are thought to reduce grazing in key resource areas (Milton & Dean 2010). The decline in grass as *L. camara* invasion increased is supported by other studies (Kumar *et al.* 2012, Prasad 2012) and it has been suggested that grass and *L. camara* may be almost mutually exclusive (Prasad 2012), although there are other factors, for example, fire and herbivory, that may also contribute to this decline of grass cover (Foxcroft *et al.* 2010). Indeed, grass composition, productivity, and spatial distribution can be modified by the presence of woody plants with their effects ranging from positive to neutral to negative depending on tree growth forms, availability of resources, extent of herbivory, and disturbances (Scholes & Archer 1997). Thus, it is simplistic to suggest that grass and *L. camara* are mutually exclusive. Invasive species may facilitate the occurrence of disturbance such as fires that promote the spread of *L. camara*, whereby *L. camara* contributes to the accumulation of fuel biomass leading to a fire-*L. camara* cycle (Hiremath & Sundaram 2005). In addition, the social-ecological processes driving *L. camara* invasion can also be attributed to various reasons that include changes to the fire regime brought about by management intervention and overexploitation of certain resources by the local human inhabitants (Sundaram *et al.* 2012). Preferred elephant foraging areas of the dry deciduous forest that were once covered with grass species like *T. triandra* and *T. cymbaria* and formed the bulk of elephant forage have now been heavily invaded by *L. camara*, with anthropogenic factors contributing to this colonization (N. Sivaganesan, pers. comm.). However, *L. camara* invasion creates a mosaic of *L. camara* and grass, with patches of original grass and gradually declining grass density with increasing *L. camara* density. Hence, elephants appear to continue to use *L. camara*-invaded habitats (Wilson *et al.* 2013) and forage on the available grass within and around *L. camara* patches. This behavior brings about changes to their feeding rates as a consequence of this invasive plant and the varying amounts of grass available at any given site. In African savannas, the lower extent of alien plant invasions was largely attributed to large mammalian herbivores, although other factors also likely contributed to invasion success (Foxcroft *et al.* 2010). Elephants foraging on grass may also contribute to the reduction in grass cover facilitating the spread and further invasion of *L. camara*. There is a lack of information on the role of elephant in facilitating the spread of *L. camara*, although their destructive feeding habits of pushing down trees and opening up the canopy are well known (Sivaganesan & Sathyanarayana 1995). Canopy gaps facilitate *L. camara* invasion by allowing more light to enter in (Totland *et al.* 2005). Studies on the African elephant have shown that high elephant density can lead to an increase in size and number of paths that open up dense vegetation and gives access to other herbivores (Kerley *et al.* 2004, Landman *et al.* 2007). In addition, these elephants were also responsible for a reduction in floral species richness through herbivory, trampling and path formation (Kerley *et al.* 2004, Landman *et al.* 2007), and nutrient cycling (Paley & Kerley 1998). Thus, both elephant and exotic weeds may have dramatic consequences on the various species of flora and fauna. Therefore, the role of elephant in facilitating the spread of invasive weeds requires further research. Such research would be particularly important if elephant populations were to increase.

Stepping rates were, however, not significantly associated with *L. camara* invasion. Instead, results from the multiple regression indicated that grass cover and browse density significantly predicted stepping rates and explained 30 percent of the total variation in the data. The path analysis allowed us to determine the importance of the direct and indirect associations of *L. camara* through grass and browse on stepping rates, which indicated a positive indirect association. The positive indirect association of stepping rates with *L. camara* may be again reflecting the reduction in grass cover and that elephants are stepping more to find grass. Alternatively, the overall negative association of *L. camara* with stepping rates, as suggested by the path analysis, indicates that possibly *L. camara* may be restricting elephant movement confining feeding to the available grass, hence resulting in reduced stepping rates.

The significant negative correlation between stepping rates and grass cover that was observed is likely to be a reflection of the availability of principal and bulk forage, which is grass. In plant communities with higher densities of preferred forage, animals are known to stay longer (Senft *et al.* 1987). Thus, elephants may have reduced their stepping rates as grass cover increased because they spent more time in one area with grass, which is their preferred forage (this study, Baskaran *et al.* 2010a), rather than moving constantly in search of more grass.

We used a path analysis because it allows for possible causal pathways for several independent variables, in addition to ranking the evident influence of potential causal factors. While similar amounts of variation were explained by multiple regression and path analysis on feeding and stepping rates (feeding rates, 7% and 9%, respectively; and stepping rates, 30% and 28%, respectively), the path analysis also provided evidence of direct and indirect effects of *L. camara* on feeding and stepping rates. This evidence, however, is correlational and does not explicitly indicate a cause–effect relationship between the variables. To untangle the effects of various factors and to properly test for causal relationships among the variables, an experimental approach is necessary.

CONCLUSIONS

The study found that wild elephants do not eat *L. camara* and is suggestive that invasive weeds such as *L. camara* are capable of modifying certain aspects of elephant behavior like feeding rates. Nevertheless, some behaviors are apparently not associated with weed invasion, for example, stepping rates. Our study suggests that if invasive weeds such as *L. camara* continue to spread, or the existing stands increase in density, grass availability for elephants and other large herbivores that depend on grass may become a constraint leading to an overexploitation of the existing grass stands. Furthermore, these grazers may facilitate further invasion by non-native woody shrubs due to the high foraging pressure they exert (Vavra *et al.* 2007).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Mudumalai Tiger Reserve in India showing locations of elephant feeding observations in the reserve within the dry deciduous forest.

TABLE S1. *The distance moved by each individual elephant during the period of observation.*

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