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Abstract

Intra and interspecific variation in frugivore behavior can have important consequences for seed dispersal outcomes. However, most information comes from among-species comparisons, and within-species variation is relatively poorly understood. We examined how large intraspecific differences in the behavior of a native disperser, blackbuck antelope *Antilope cervicapra*, influence dispersal of a woody invasive, *Prosopis juliflora*, in a grassland ecosystem. Blackbuck disperse *P. juliflora* seeds through their dung. In lekking blackbuck populations, males defend clustered or dispersed mating territories. Territorial male movement is restricted, and within their territories males defecate on dung-piles. In contrast, mixed-sex herds range over large areas and do not create dung-piles. We expected territorial males to shape seed dispersal patterns, and seed deposition and seedling recruitment to be spatially localized. Territorial males had a disproportionately large influence on seed dispersal. Adult males removed twice as much fruit as females, and seed arrival was disproportionately high on territories. Also, because lek-territories are clustered, seed arrival was spatially highly concentrated. Seedling recruitment was also substantially higher on territories compared with random sites, indicating that the local concentration of seeds created by territorial males continued into high local recruitment of seedlings. Territorial male behavior may, thus, result in a distinct spatial pattern of invasion of grasslands by the woody *P. juliflora*. An ex situ experiment showed no beneficial effect of dung and a negative effect of light on seed germination. We conclude that large intraspecific behavioral differences within frugivore populations can result in significant variation in their effectiveness as seed dispersers. Mating strategies in a disperser could shape seed dispersal, seedling recruitment and potentially plant distribution patterns. These mating strategies may aid in the spread of invasives, such as *P. juliflora*, which could, in turn, negatively influence the behavior and ecology of native dispersers.

An intriguing feature of species interactions is the opportunity for each actor to influence trait evolution and ecological properties in the other. The interaction between plants and their animal dispersers, for example, can influence the evolution of plant traits such as fruit color, fruit chemistry, crop size and the timing of reproduction (Herrera 1982, Tewksbury et al. 2002). Since seed dispersal can also influence downstream processes, such as seed survival, and seedling and sapling recruitment (Wang and Smith 2002), animal dispersers can also have crucial effects on plant abundance and dispersion and thereby on plant population, and community dynamics (Howe and Miriti 2004, Seidler and Plotkin 2006). So, the interaction between plants and their dispersers can have both evolutionary and ecological consequences.

All dispersers are not alike and effective seed dispersal of a plant can vary widely among its dispersers (Jordano et al. 2007). Dispersers often differ in the quantity of fruit they remove (Howe and Primack 1975, Prasad and Sukumar 2010), the ways in which they process seeds in their digestive tract (Traveset et al. 2001), in their patterns of seed deposition and in the subsequent probability of seed establishment (Dennis and Westcott 2007, Jordano et al. 2007). Such variation among dispersers in their effects on seed dispersal has been shown to result from differences in, among other things, disperser movement patterns, ranging behavior, feeding preferences and feeding behavior (Wenny and Levey 1998, Westcott et al. 2005, McConkey and Drake 2006, Russo et al. 2006, Campos-Arceiz et al. 2008). Thus, animal behavior can affect plant population structure through its effects on seed dispersal.

Attempts to incorporate animal behavior into estimating seed dispersal have largely been restricted to examining interspecific variation in disperser behavior (Wenny and Levey 1998, Dennis and Westcott 2007, Jordano et al. 2007). But dispersers often also display considerable within-species variation in movement and foraging behavior and such intraspecific variation in animal behavior could have important consequences for seed dispersal patterns (Rawsthorne et al.

2011). Intraspecific variation in ranging and feeding is expected to be widespread and driven by various evolved differences between individuals of a population, such as in body size and in group formation (smaller groups may range less than larger groups) (Jarman 1974, Balmford 1992). Some of the greatest behavioral variation between individuals in a population can arise from differences between the sexes, and even between individuals of the same sex but following different reproductive strategies. Breeding males, particularly in highly sexually selected species, often show substantial differences in feeding and ranging behavior compared with non-breeding males and females. For example, in antelope and several birds where males defend small mating territories and court and try to mate with females visiting these territories, males feed and move over much smaller areas than do females (Balmford 1992, Thery 1992, Hingrat et al. 2004, Isvaran 2007). Such intraspecific variation in movement and feeding behavior can lead to differences in the spatial patterns of seed dispersal by different types of social categories (Rawsthorne et al. 2011), and also in subsequent seed survival probabilities.

Understanding the impact of intraspecific variation on seed dispersal could be particularly important in conservation contexts, such as managing threatened or invasive species (Myers et al. 2004), by making search efforts more efficient and by identifying appropriate search zones for eradication (Westcott et al. 2008). Motivated by this, we studied the influence of variation in social behavior of the blackbuck antelope *Antilope cervicapra* on seed dispersal of a woody invasive *Prosopis juliflora* (mesquite, Fabaceae) in a semi-arid grassland in western India.

Prosopis juliflora, native to central and south America, is a highly invasive woody plant (Pasiecznik et al. 2001), mainly affecting grassland habitats, and converting them into scrublands and woodlands (Archer 1989). It was intentionally introduced in many parts of the world to provide fuel-wood, and prevent droughts and desertification (Pasiecznik et al. 2001). It appears to be assisted in its spread by native herbivores (Shiferaw et al. 2004). *Prosopis juliflora* bears hard-coated seeds within nutritious indehiscent pods which are readily eaten by both domestic and wild ungulates and dispersed through their dung (Pasiecznik et al. 2001, Shiferaw et al. 2004).

Blackbuck, the dominant ungulate species in many semi-arid grasslands across India (Ranjitsinh 1989), disperse *P. juliflora* seeds (Jhala 1997), and may play an important role in aiding the spread of *P. juliflora*. Blackbuck show marked individual differences in foraging and ranging behavior as a consequence of social and mating strategies. They are largely group-living, with the exception of territorial males that defend mating arenas in open areas. Behavior relevant to seed dispersal, i.e. movement and foraging, differs greatly among the different types of blackbuck social categories. These differences are most extreme where the rare mating strategy, lekking, is dominant.

In lekking populations of blackbuck, most breeding males defend small territories which are clustered to form an aggregation known as a lek. Some males may also defend larger, dispersed territories (Isvaran and Jhala 2000, Isvaran 2005a, b). Breeding male blackbuck generally show restricted movement, spend most of their time on their territories, and when they leave their territories to feed they do so close by. In contrast, female and bachelor male herds range and feed over much larger areas. As in many antelopes, territorial male blackbuck display a striking scent-marking behavior, which results in large spatially- restricted concentrations of dung in the landscape. Males regularly defecate at particular locations within their territories forming dung-piles. Where territorial males aggregate into leks, these dung-piles are clustered close to each other; where territories are loosely aggregated or not aggregated at all, dung-piles are widely separated from each other. Individuals in female and bachelor male herds do not exhibit such scent-marking behavior, and dung-piles are rarely seen outside territories.

We examined the influence of the behavioral differences in blackbuck, arising from extreme mating strategies of males, on different stages of the seed dispersal process in *P. juliflora*, specifically fruit removal, seed deposition and seedling recruitment. We first examined the quantities of *P. juliflora* fruit removed by different frugivore species and by different age-sex groups of blackbuck. We next evaluated seed deposition and seedling recruitment patterns. We expected territorial males to strongly shape seed dispersal patterns in the landscape as a consequence of their movement and marking behavior. Because territorial males show restricted movement and regularly defecate on dung-piles on their territories, we hypothesized that seed deposition in the landscape would be spatially localized; hence, we predicted that seed deposition should be far greater on territories than on random sites in the grassland and shrubland area used dominantly by herds. We assessed whether our expectation of high seed deposition continued into high seedling recruitment by comparing seedling abundances on territories with those on random sites in grasslands and shrublands. We checked the assumption that territorial males are responsible for seeds deposited on territories, and herds for seeds deposited outside territories, by monitoring use of these areas by the herds and territorial males.

Territorial males may also direct seed dispersal patterns by bringing seeds to more suitable microsites for seed germination and growth. Dung-piles have higher light and dung availability, and lower grass cover, and may thus provide better resources for seed recruitment. As a first step towards examining this mechanism, we conducted an ex situ experiment to test the effect of light and dung conditions on seed germination. We discuss the implications of our findings for the process of spread of *P. juliflora* and for management of grassland habitats invaded by woody species.

Material and methods

Study area

This study was conducted in Velavadar National Park (21°56′N, 72°10′E, 34.5 km²), Gujarat, India, from January to May 2010. Velavadar mainly consists of semi-arid grassland interspersed with saline mudflats and *Prosopis juliflora* shrublands. *Prosopis juliflora*, introduced about 90 years ago, is the only prominent woody plant at Velavadar, and covers 50% of the original grassland habitat (Jhala 1997). *Prosopis juliflora* was initially planted in and around Velavadar to provide

fuel-wood for local human communities. Since then it has spread across the landscape, dispersed presumably both by wild and domestic ungulates (Jhala 1997). Since the declaration of Velavadar as a protected area in 1969, use of the area by domestic ungulates has been minimal (Priyadarshini 2005). Even though cattle have played an important role in the dispersal of *P. juliflora* in Velavadar in the past, on-going seed dispersal and seedling recruitment patterns are not expected to be influenced by domestic ungulates.

Three native ungulates are found here–blackbuck, nilgai *Boselaphus tragocamelus* and wild pig *Sus scrofa*. Of these, blackbuck is the most closely associated with the grassland habitat (Ranjitsinh 1989). Blackbuck depend on the grassland for their food and the defense of mating territories. Their diet primarily consists of grass, with *P. juliflora* pods forming about 10% of their annual diet (Jhala 1997). Velavadar holds one of the largest concentrations of blackbuck in India (1642 individuals, Gujarat Forest Dept. Census 2010). Female blackbuck are typically found in female-biased herds (two to many hundred in size, Isvaran 2007), which are composed of females of all age classes and juvenile males, and may (mixed-sex herds) or may not (female herds) contain adult males; whereas males are found in all-male (no females) or mixed-sex herds, or defend mating territories in open habitat. Velavadar has one large lek with a high density of small, clustered territories (> 50 territories during peak mating season), hereafter lek territories. Elsewhere in Velavadar are smaller clusters of dispersed territories and solitary territories (Isvaran and Jhala 2000; hereafter dispersed territories).

Our study period encompassed the fruiting season of *P. juliflora* (peak: Dec.–Jan.; additional fruiting throughout the year) and the blackbuck mating season (peak: March– April, with low levels of additional mating activity from December to February and in May; Isvaran and Jhala 2000).

Visits and removal rates of *P. juliflora* pods

To estimate the proportion of *P. juliflora* pods removed by different ungulate species, and by different age-sex classes of blackbuck, we used a time-delay camera-trap technique (Prasad et al. 2010). A remotely triggered passive-infrared digital camera trap was set focussed on 1–10 freshly fallen pods under focal *P. juliflora* trees. The camera-trap was programmed to take four pictures at 0, 2, 4 and 6 min upon trigger (by a moving animal), yielding a time delay sequence of photographs. By comparing the number of fruits remaining across this sequence, it was possible to verify if the visiting animal had consumed fruits and also estimate the number of pods removed by frugivorous animals.

To examine variation in visits and pod removal, we selected focal trees in two distinct habitats: open areas and *P. juliflora* thickets (i.e. with other *P. juliflora* trees within 10 m of the focal tree). None of the sampled focal trees were on male mating territories, since males typically defend territories in open tree-less areas. We conducted camera trapping during peak mating (March) and late peak mating season (April). Camera-traps were monitored once daily for a maximum of two days. Trees were resampled only after a gap of two weeks. Photographs were examined carefully to identify frugivores. A frugivore visit was defined as an event when a frugivore species was photographed under a *P. juliflora* tree. A removal event was defined as a visit during which *P. juliflora* pods were observed to be removed by the visiting frugivore through the time-delay sequence of pictures.

Seed deposition and seedling recruitment

We quantified spatio-temporal variation of *P. juliflora* seed deposition by blackbuck and seedling recruitment using a spatially stratified random sampling design. To ensure that the different broad habitat types were adequately sampled, we first broadly stratified Velavadar based on vegetation composition into sparse grassland, dense grassland, sparse *P. juliflora* scrub, dense *P. juliflora* scrub, and mudflat. Random locations were then generated in these habitat types using Quantum GIS mapping software (ver. 1.3.0-Mimas). At each random location, one of the eight cardinal directions was chosen at random to lay a transect. Along each transect, we set 1–3 plots (2 × 2 m), two hundred metres apart from each other (Figure 1a).

Because blackbuck territories form a small fraction of the total landscape, we separately focussed on territories to identify and sample lek and dispersed territories (Figure 1b–c). A subset of these territories was randomly selected using Quantum GIS. Within each territory, a 2 × 2 m plot was laid on one of the main dung-piles; the geometric centre of the dung-pile was taken as the centre of the plot. In addition, a second plot was laid 5 m away from the centre of the plot on the dung-pile in one of the eight cardinal directions selected at random (Figure 1b–c). If this second plot overlapped another dung-pile, the plot was instead moved to another randomly chosen direction. In this way, we laid one plot on and one off a dung-pile on each sampled territory to examine the effect of exaggerated scent-marking behavior of territorial males on seed deposition.

Within each 2 × 2 m plot we measured habitat variables, blackbuck dung density, and *P. juliflora* seed and seedling densities. All plots were monitored twice, in early peak blackbuck mating season (Jan.–Mar.) and in the late blackbuck mating season (April). At two extreme ends of each plot (N–S or E–W, alternated across plots) a 0.5 × 0.5 m grid with 25 equally spaced points was placed on the ground vegetation.

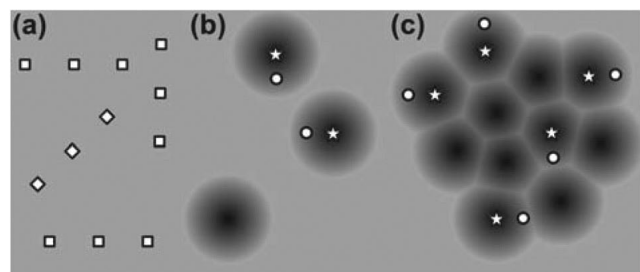
Figure 1. Schematic diagram of the sampling design (a, b and c). Increasing darkness represents increasing blackbuck dung density (see methods). In non-territorial areas (random sites), plots (squares) were laid in a stratified-random fashion (a). In territorial areas, plots were laid on dung-piles (star) and off-dung piles (circle) within dispersed territories (b) and lek (c) territories.

Grass cover was measured as the number of points in the grid intersecting with grass shoots, and grass height was measured at two diagonally opposite points in the grid. The distance of each plot from the nearest tree (greater than 1.5 m in height, which for 76% of the plots was *P. juliflora*) was estimated through paces.

In each 2 × 2 m plot, blackbuck dung density was estimated in two 0.5 × 0.5 m grids as the number of grid points that intersected fresh blackbuck pellets (henceforth 'dung density index': minimum = 0, maximum = 2 × 25 = 50 per plot). Blackbuck pellets were easily distinguished from droppings of other sympatric ungulates by size and shape and were classified into fresh (black or brown) or old (mostly white and cracked) groups. Only fresh pellets were used to calculate the dung density index so that this measure reflects recent (less than six months) use by blackbuck that we could then correlate with seed deposition from the current *P. juliflora* fruiting season. As we also examined seedling recruitment which could have resulted from seed deposition by blackbuck over a longer period and not just the current fruiting season, we also estimated 'total dung density' by using both fresh and old pellets to measure longer term use of the area by blackbuck.

In each 2 × 2 m plot, fresh pellets were collected from throughout the plot and opened to examine *P. juliflora* seeds contained within. In plots with fewer pellets than that equivalent to three defecations, up to twenty pellets were opened (or all pellets if fewer than twenty were present), while in plots with more pellets than that equivalent to three defecations, 60 pellets were opened. Within plots on dung-piles (which had very high dung density), 100 pellets were opened. All *P. juliflora* seedlings were counted in each 2 × 2 m plot.

Habitat use by blackbuck social categories

To evaluate our assumption that seeds found on territories were most likely to have been deposited by territorial males, while those found on random plots were most likely to have been deposited by all-male and female-biased herds, we estimated the use of these habitats by the different social categories. We carried out scan sampling throughout the study period using a spotting scope and binoculars from three watch towers, chosen to provide good coverage of the different habitat types in the landscape. At each watch tower, we carried out three two-hour scan sessions, randomly selected to represent three parts of the day: morning (06:30–10:30 h), afternoon (10:30–14:30 h) and evening (14:30–18:30 h). Three such sets of replicates were taken. Blackbuck are diurnal, and activity at night is limited (Ranjitsinh 1989). During each scan the different habitat patches (grassland, sparse *P. juliflora* scrub, dense *P. juliflora* scrub, dispersed territories and lek territories) were scanned at 10 min intervals and the number of individuals of different social categories (all-male herds, female-biased herds, territorial males) was recorded.

Factorial germination experiment

To examine how seed germination is affected by blackbuck ingestion and by micro-habitat conditions at deposition sites, an ex situ factorial experiment (Sánchez de la Vega and Godínez-Alvarez 2010) was carried out in Vadodara, Gujarat, India, from March to May 2010.

Eight hundred intact seeds were collected with 100 seeds for each treatment combination of ingestion (ingested vs non-ingested seeds) and micro-habitat (dung vs no dung and light vs shade). We expected ingested seeds in dung to germinate faster due to scarification in the gut of the disperser, and favorable conditions provided by the dung along with which the seed is deposited. We also expected that seeds in light (for example, on dung-piles which are open areas with little or no grass) would germinate faster than seeds in shade (in grassland areas where grass blades prevent light from reaching the seed). Ingested seeds were collected from blackbuck dung-piles found in plots at the field site. Non-ingested control seeds were removed manually from fallen pods collected from at least 15 *P. juliflora* trees. A natural control treatment of 40 whole *P. juliflora* pods was also used. For the dung treatment, seeds were placed in coarsely broken blackbuck pellets equivalent of one pellet. For the shade treatment, seeds were placed under a green mesh shade cloth. Ten germination trays had sand-filled sockets, which held individual seeds, and treatments were assigned to sockets systematically across trays by alternating treatments across sockets in each tray. Each tray had equal representation of ingestion and dung treatments and half the trays were placed under shade. The trays were watered twice a day to ensure that they remained moist and were checked every day for germination, defined as visible radicle protrusion.

Analysis and results

All statistical analyses were carried out using the statistical and programming software R (ver. 2.15.1; R Development Core Team). Statistical inferences were based on model selection using an information theoretic approach (Burnham and Anderson 2002). For each analysis, a candidate set of models, which represented different ecological hypotheses, was specified and fitted to the data. The relative fit of different models within the candidate set was evaluated using the corrected Akaike's information criterion (AICc). The model with the smallest AICc is the best estimate, based on the data, of the unknown 'true' model. Where there was a clear difference between the best model and the rest of the models in the candidate set (smallest ΔAICc > 10) then parameter estimates and confidence intervals for predictors were based on the best model. However, when differences between models were not so clear (ΔAICc < 2), then inferences were based on multiple models, i.e. using model averaged parameter estimates and confidence intervals (Burnham and Anderson 2002). Mean ± SEs are shown unless otherwise indicated. For non-normal data bootstrapped confidence intervals are shown.

Are blackbuck important dispersers of *P. juliflora* seeds?

We evaluated frugivory by different terrestrial frugivores using camera trap data from 38 trap days at 27 focal

Prosopis juliflora trees. We compared 1) the proportion of total visits and 2) the proportion of fruits removed by the different frugivore species by examining binomial means and confidence intervals. Across the 38 trap days, 91 ungulate visits were noted at *P. juliflora* trees; out of these, 45 resulted in pod removal. Among the ungulates, blackbuck visited most frequently, comprising nearly 50% of the total visits (mean proportion = 0.484; 95% CI = 0.378–0.590; n = 44 of a total of 91 ungulate visits), followed by *S. scrofa* (mean = 0.341; 95% CI = 0.247–0.448; n = 31) and *B. tragocamelus* (mean = 0.176; 95% CI = 0.107–0.273; n = 16). One hundred and fifty two of the 176 fruits laid out were removed; the three ungulate species were the only terrestrial frugivores recorded. The proportion of fruit removed by blackbuck (mean = 0.39; 95% CI = 0.311–0.471; n = 59 of a total of 152 fruits removed by frugivores) was similar to that taken by *S. scrofa* (mean = 0.382; 95% CI = 0.305–0.464; n = 58) and higher than that taken by *B. tragocamelus* (mean = 0.23; 95% CI = 0.168–0.307; n = 35). Removal rate of pods in the study area was very high and all available freshly fallen pods (that the camera traps were focused on) were removed when they were relatively fresh, within 24 h for 80% of the sampled trap days.

What is the pattern in fruit removal by blackbuck of different sex and age classes?

Assessing frugivory by different blackbuck age and sex classes, the frequency of visits by adult males (mean = 0.545; 95% CI = 0.39–0.693; n = 24 of a total of 44 visits by blackbuck) was higher than that by females (mean = 0.341; 95% CI = 0.209–0.5; n = 15), while those by immature males was very low (mean = 0.068; 95% CI = 0.018–0.2; n = 3; age and sex of two blackbuck individuals could not be identified from photographs). Adult blackbuck males removed more than twice as much fruit than did females (males: mean = 0.661; 95% CI = 0.525–0.776; n = 39 of a total of 59 fruits removed by all blackbuck; females: mean = 0.254; 95% CI = 0.154–0.387; n = 15). Immature males removed very little fruit (mean = 0.085; 95% CI = 0.032–0.194; n = 5).

Seed deposition

As *P. juliflora* seeds are dispersed through dung, we expected seed presence to be closely tied to dung deposition, and therefore, we carried out paired sets of analyses, with the response variable in one member of each pair being amount of dung and the response variable in the other being seed presence. Our measure of the amount of dung is the dung density index described earlier. Because the vast majority of plots (234 out of 267) examined had no seeds (mean = 0.33, SD = 1.27, range = 0–13, n = 267), and because out of the 33 plots with seeds 17 contained only one seed (mean number of seeds = 2.64, SD = 2.68, range = 1–13, n = 33), we coded seed presence as simply present or absent, rather than using the actual counts. In our analysis of these questions, we focus on blackbuck dung, because our research question focuses on the interaction between this ungulate and *P. juliflora* and on establishment of this woody invasive in grassland habitats. Our findings support this focus on blackbuck dung as blackbuck removed substantial

amounts of fruit. Additionally, blackbuck were dominant in the area (of the 267 plots, 237 had blackbuck dung as against 41 with *B. tragocamelus* and 12 with *S. scrofa* dung) particularly in grasslands, thereby suggesting that the other frugivores are unlikely to have as great an impact on *P. juliflora* dispersal patterns even though *S. scrofa* consumed substantial amounts of fruit.

Is dung abundance and seed presence greater on vs off territories?

To test our main hypothesis, that territorial males strongly shape seed deposition patterns through their restricted movement and marking behavior which is expected to concentrate dung and therefore seeds on to territories, we began by asking whether dung abundance is different on versus off territories. We did this by running a zero-inflated binomial generalized linear model (GLM) with dung density index as the response variable and location (on or off a territory) as the predictor. Dung density index was bounded by 0 and 50 and hence we used a binomial error structure with the response variable coded as the number of points in a plot with dung out of a total of 50 points. As dung was absent in many plots we used zero-inflated models. In parallel, to test whether, corresponding with dung patterns, seed arrival varies on and off territories, we ran a GLM with binomial errors with seed presence/absence as the response variable, location as a predictor, and two additional predictors: 1) local *P. juliflora* density, measured as the distance to the nearest *P. juliflora* tree, used because we expected the probability of there being seeds in a plot to fall with increasing distance to the nearest *P. juliflora* tree; and 2) season, used because the feeding and dung deposition behavior of blackbuck might vary with time in the mating season.

Dung density index was substantially higher on territories (mean = 17.2, SD = 17.8, range = 0–49, n = 92) than at locations off territories (mean = 0.6, SD = 1.3, range = 0–8, n = 175). The zero-inflated binomial GLM with plot location (on vs off territories) performed considerably better (ΔAICc = 1160.9) than a null (intercept only) model without plot location.

Similarly, the probability of a seed being present on a plot was considerably higher (four times as high) on versus off territories, and there was no additional effect of local *P. juliflora* density or season (Table 1). Because seed presence was abysmally low off territories (only nine of 175 plots off territories had seeds), and by far the greatest proportion of plots with seeds was on territories (24 of 92 plots), we discarded plots off territories in further analyses and focussed on examining patterns in seed deposition within the plots on territories.

Does dung abundance and seed presence vary between lek and dispersed territories and also, between plots on vs off dung-piles within a territory?

In the next pair of analyses, we examined whether dung abundance and seed deposition differed between lek territories and dispersed territories, and within these territories, between plots on dung-piles and those off dung-piles. To account for the paired design of plots (on and off dung-piles)

Table 1. Analysis of seed presence on versus off territories: top candidate models (within 2 AICc units of best model) and model averaged parameter estimates with 95% CI from a GLM with binomial errors. To show the magnitude of the effect of different predictors, we calculated the percent change in seed probability for a given change in a predictor, difference between levels for categorical variables and difference between the 1st and 3rd quartiles for continuous variables; when calculating percent change in seed probability for a particular predictor, the other predictors are kept constant (categorical variables at the intercept level and continuous variables at their median value). DF = degrees of freedom. AICc = corrected Akaike information criterion. w = Akaike weight.

Candidate model syntax	DF	Log likelihood	AICc	ΔAICc	w
Location (on/off territories) + Season	3	−86.59	179.28	0	0.45
Location (on/off territories)	2	−88.28	180.6	1.32	0.23
Location (on/off territories) + Local *P. juliflora* density + Season	4	−86.43	181	1.73	0.19

Parameter	Estimate	CI lower limit	CI upper limit	% change in seed probability
Intercept (Location–off territory and Season–late lekking)	−3.20	−4.08	−2.32	
Location (on territory)	1.85	1.00	2.70	418%
Season (early lekking)	0.72	−0.08	1.51	96%
Local *P. juliflora* density	0.00	−0.003	0.01	13%

within the same territory, we used generalized linear mixed effects models (GLMM) with binomial error structure and with dung density index as a response variable in one GLMM and seed presence/absence as the response variable in the other GLMM. In both GLMMs, territory type (lek vs dispersed) and location within territory (on dung-pile versus off dung-pile) were used as predictors, together with an interaction term, and territory identity was used as a random effect. As before, local *P. juliflora* density and season were additional predictors for the analysis with seed presence as the response variable.

Dung abundance was much higher (as expected) on dung-piles (mean = 32.15, SD = 13.24, range = 0–49, n = 46) than off dung-piles (mean = 2.2, SD = 3, range = 0–13, n = 46) and this difference was greater on dispersed territories (see GLMM results in Supplementary material Appendix 1 Table A1). The pattern in seed presence was similar to that in dung abundance. Seeds were more likely to be found on rather than off dung-piles; however, there was no effect of territory type or local *P. juliflora* density (Table 2). In addition, seed presence was greater in the early lekking season than in the late lekking season.

Which social categories are most common on territories and on random sites off territories?

We used data from scan samples to check whether dung on territories is deposited largely by territorial males and dung in off-territory plots in grassland and shrubland is deposited by non-territorial individuals (mostly in herds). We did this by comparing the relative frequencies of individuals belonging to the different social categories on and off territories and assuming that relative frequencies correlate with the amount of dung deposited. As the purpose of this analysis was to check whether seeds found in dung in territorial areas could be attributed to territorial males (unlike some other ungulate species, e.g. black lechwe *Kobus leche*, in which herds too spend a large amount of time on territories) and similarly whether herds dominated off-territory areas, we compared means and confidence intervals (bootstrapped as data were non-normal) to make inferences.

A large proportion of the blackbuck population was found in the grassland area. Blackbuck social categories were fluid in nature and group size varied considerably through the day. During some periods of high foraging activity, female-biased groups and all-male groups frequently used the same grassland patch such that the two social categories were observed to merge to form one large female-biased group. Because much of the population aggregated from time to time into relatively few large groups, many grassland patches were temporarily empty, and this is reflected in the large variance in the number of individuals observed in focal areas at any particular point in time (Figure 2). A comparison of the relative frequencies of individuals belonging to different social categories in a habitat type indicated that a) at random sites in grassland and shrubland, individuals belonging to female-biased groups followed by those in all-male groups were most frequent, b) dispersed territories were dominated by territorial males, followed by female-biased groups, and c) the lek was dominated by territorial males, followed by female-biased groups (Figure 2).

What explains variation in seedling recruitment in the landscape?

The number of *P. juliflora* seedlings in an area should be a function of seed deposition (examined above) and seed survival. We expected seed survival to be influenced by (among other things) dung abundance, grass cover and local *P. juliflora* density. To evaluate this hypothesis, we modelled the number of *P. juliflora* seedlings in a plot as the response variable in a GLM with negative binomial errors (to account for over-dispersion). The predictors were total dung density (which included both old and fresh pellets; total dung density was used since the seedlings could have come through both recent and old pellets), local *P. juliflora* density, grass cover and season. We did not include territory type as a separate predictor because dung abundance is strongly correlated with territoriality.

During both early and late peak mating season approximately 14% of the plots had seedlings, and the maximum number of seedlings in a plot was 30. When trying to explain

Table 2. Analysis of seed presence between lek and dispersed territories (DT) and also, on versus off dung-piles within a territory: top candidate models (within 2 AICc units of best model) and model averaged parameter estimates with 95% CI from a GLMM with binomial errors. DF = degrees of freedom. AICc = corrected Akaike information criterion. w = Akaike weight.

Candidate model syntax	DF	Log likelihood	AICc	ΔAICc	w
Location (on/off dung-pile) +Season	4	−46.84	102.13	0	0.4

Parameter	Estimate	CI lower limit	CI upper limit
Intercept (Territory–DT, Location – off dung-pile and Season–late lekking)	−2.27	−3.62	−0.92
Location (on dung-pile)	1.21	0.052	2.37
Season (early lekking)	1.27	0.22	2.32
Local *P. juliflora* density	−0.0009	−0.01	0.004
Territory (lek)	−0.08	−1.48	1.32
Territory (lek): Location (on dung-pile)	0.8	−1.35	2.96

variation in the number of seedlings in a plot, no single 'best' model (ΔAICc > 10 units) was identified, hence inferences were based on model averaged parameter estimates and CIs (Table 3). Overall, number of seedlings was related only to dung abundance: plots with more dung had more seedlings (Table 3). The number of seedlings was not related to grass cover, local *P. juliflora* density, or to mating season.

Taken together, the results from this and the previous section indicate that seedlings were related to dung abundance and that dung abundance was substantially higher on versus off territories, As might be expected from these results, the number of seedlings in a plot was strongly related to the territorial nature of the plot. Seedling numbers were highest on the lek, twice that on dispersed territories. In comparison, random sites in grassland and *P. juliflora* shrubland had very low number of seedlings per plot (Figure 3).

Do conditions at dung-piles favour seedling recruitment?

To examine the effect of experimental conditions of light, dung and ingestion on 1) the probability of seeds germinating and 2) the latency (number of days) in germinating, GLMs with binomial and Poisson errors were used respectively.
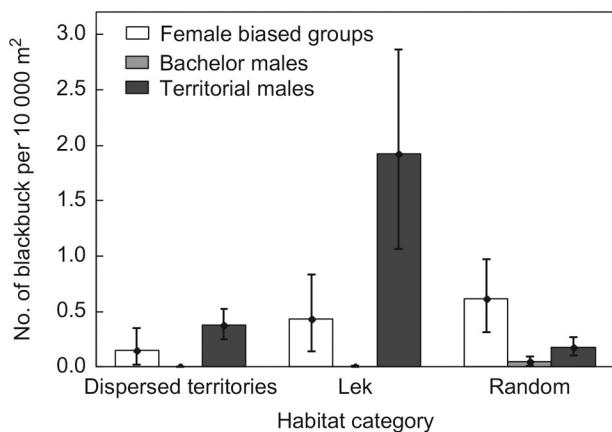

Figure 2. Frequencies of individuals belonging to different social categories in territorial areas (dispersed territories and lek) and non-territorial areas (random sites in grassland and shrubland). Error bars show bootstrapped 95% CI (n = 27 × 3 h watches).

Light (unshaded vs shaded), dung (present vs absent), ingestion of seeds (seeds from dung vs hand removal of flesh alone) and all two-way interactions were included as predictors.

Out of 800 seeds that were sown, 26% were lost or discarded due to the presence of more than one seed in a single slot (which arose accidentally during watering or with strong wind conditions). Of the remainder, 58% (343 seeds) germinated. None of the *P. juliflora* pods in the 'natural' control treatment showed any signs of rotting of the pericarp and liberation of the seeds, and so no seeds germinated in this treatment. Examining the success in seeds germinating and days to germination, no single 'best' model (ΔAICc > 10 units) was identified, hence model averaged parameter estimates and 95% CIs are presented. Light conditions influenced the probability of seeds germinating the most; germination of seeds was 30–50% higher in shade than in full light (Figure 4a, Table 4). Presence of dung did not greatly affect the germination of seeds. Germination of ingested seeds was similar to that of non-ingested seeds prepared by hand removal of flesh alone. Of the seeds that germinated, seeds under shade germinated earlier than those in full light (Figure 4b, Supplementary material Appendix 1 Table A2). Irrespective of light conditions, seeds germinated earlier in the absence of dung than in the presence of dung. Ingestion of seeds by blackbuck did not influence the number of days to germination of seeds.

Discussion

Our findings suggest that large behavioral differences between individuals of a species, arising from extreme male mating strategies, can result in significant variation in their effectiveness as seed dispersers. Breeding males, despite forming a relatively small proportion of the population (approximately 8%; Isvaran and Jhala 2000, Isvaran unpubl.), had a disproportionately large influence on seed deposition and seedling recruitment. Furthermore, we found that the extreme territoriality (lekking) shown by breeding males in the study population can result in striking spatial patterns in dispersal. These findings illustrate a relatively unexplored mechanism by which mating strategies of animal dispersers can influence the ecology of the plants they disperse, and

Table 3. Analysis of seedling recruitment in the landscape: top candidate models (within 2 AICc units of best model) and model averaged parameter estimates with 95% CI from a GLM with negative binomial errors. To show the magnitude of the effect of different predictors, we calculated the percent change in seedling numbers for a given change in a predictor, difference between levels for categorical variables and difference between the 1st and 3rd quartiles for continuous variables; when calculating percent change in seedling probability for a particular predictor, the other predictors are kept constant (categorical variables at the intercept level and continuous variables at their median value). DF = degrees of freedom. AICc = corrected Akaike information criterion. w = Akaike weight.

Candidate model syntax	DF	Log likelihood	AICc	ΔAICc	w
Total dung index	2	−182.3	368.65	0	0.31
Grass cover + Total dung index	3	−181.88	369.86	1.21	0.17
Season + Total dung index	3	−182.04	370.17	1.52	0.15
Local *P. juliflora* density + Total dung index	3	−182.09	370.27	1.62	0.14

Parameter	Estimate	CI lower limit	CI upper limit	Percent change in seedlings
Intercept (Season–late lekking)	−1.47	−2.37	−0.58	
Total dung index	0.06	0.03	0.10	38%
Grass cover	0.06	−0.10	0.21	38%
Season (early lekking)	−0.29	−1.42	0.84	−25%
Local *P. juliflora* density	0.00	−0.01	0.00	−17%

emphasize the importance of considering intraspecific heterogeneity in dispersal patterns by animal dispersers. These findings also have potential management implications, providing insights into how a woody invasive is likely to spread in a grassland landscape.

Intraspecific variation in fruit removal

Variation between individuals in their influence on seed dispersal stages was already apparent at the fruit removal stage. Adult male blackbuck appeared to play a disproportionately large role in *Prosopis juliflora* pod removal. Adult males removed twice as much fruit compared to females although frequency of visits by adult males and females were not different, and there are three times as many females as adult males in this population (Isvaran 2005a). This pattern may reflect a greater propensity of adult males to adopt costly but energetically rewarding foraging behavior. Blackbuck rely on early detection and flight to avoid predators and have been shown to prefer open grassland habitats (Jhala 1997) over shrublands and appear to perceive habitat with woody cover as risky areas (Isvaran 2007). However, because territorial males experience high costs associated with defending these mating territories, territorial males may be relatively more willing to spend time in 'risky' habitats to forage on the nitrogen rich pods. As camera traps were used to quantify visitation and removal, and males in our population were not individually identified, we were

Figure 3. Seedling recruitment in dispersed territories, lek territories and random sites. Error bars show bootstrapped 95% CI (n = 267 plots).

unable to determine which adult males visiting the focal trees were territorial; therefore, the foraging strategies of territorial males versus other categories of individuals remain to be explored. Additionally, peak *P. juliflora* fruiting (Dec.–Jan.) is outside the peak blackbuck mating season. However blackbuck breed through the year including during the peak *P. juliflora* fruiting season, during which there are 10–20 males maintaining territories on the lek and a few males on dispersed territories. Therefore, we expect patterns in fruit removal and seed dispersal in Dec.–Jan. to be similar to the patterns we found during our study but perhaps not as strong; this remains to be examined.

Camera trap observations also showed that *S. scrofa* removed substantial amounts of fruit. However, *S. scrofa* used grasslands very infrequently resulting in very low seed dispersal into grasslands by this ungulate (2.6% of plots had seeds dispersed through *S. scrofa* dung compared with 12.4% of plots that had seeds dispersed in sampled blackbuck pellets). Also, pigs often destroy seeds upon ingestion (Pasiecznik et al. 2001, Prasad S. pers. obs.), thereby reducing their effectiveness as dispersers. Hence, their role in *P. juliflora* dispersal into grasslands is likely to be small.

The proportion of pods consumed in an event of removal was high for all frugivores and across age-sex classes of blackbuck. In the germination experiment, none of the whole pods in the 'natural control' treatment showed any signs of seed liberation or germination, indicating that ingestion by frugivores was essential to liberate seeds from the indehiscent pods. The relatively short duration of our germination experiment (three months) may have been too short to show signs of seed liberation from the indehiscent pods in our 'natural control'. However, if *P. juliflora* seeds are not liberated from pods for extended periods, they are unlikely to germinate as a result of either destruction by insect predators, lack of moisture owing to the hard exocarp of the fruit, or damage by fungal attack in the event of submergence in water during the wet season (Pasiecznik et al. 2001). Whole pods have been used for cultivation of *P. juliflora* by either depositing them deep in the soil or soaking them in water for several days, resulting in low germination and establishment
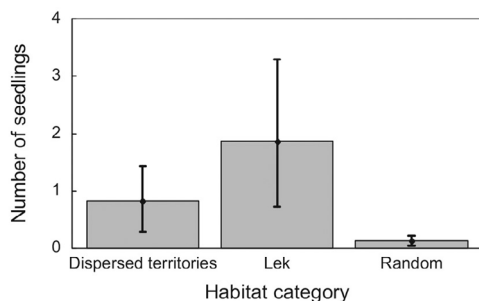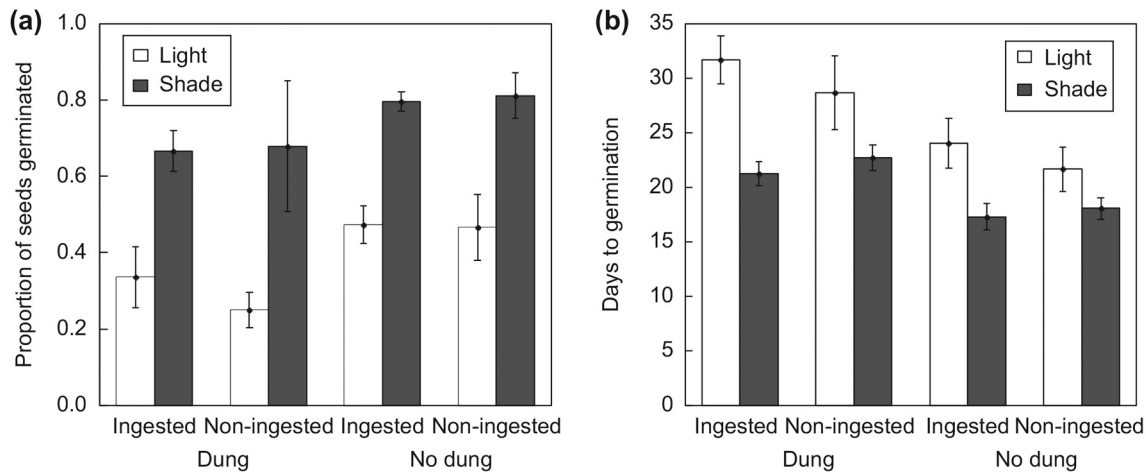
Figure 4. Proportion of seeds germinated (a) and germination latency in days (b) of *P. juliflora* seeds under treatments of ingestion (ingested or non-ingested), dung (presence/absence) and light (under light/shade). Error bars show SE.

rates (Pasiecznik et al. 2001). Apart from seed liberation, the removal of pods by frugivores may provide an escape to the seed (Howe and Smallwood 1982) from insect seed predators near the parent tree (Jadeja unpubl.). A study on a related species, *Prosopis ferox*, found minimal pod removal by frugivores; none of the seeds were liberated from the indehiscent pods and 99% of the seeds within the pods remaining under parent plants were depredated by bruchid insects over a period of six years (Baes et al. 2002).

Blackbuck territoriality and seed dispersal patterns

Territorial male behavior resulted in movement of seeds to sites away from existing *P. juliflora* clumps into grasslands. Consistent with our expectation, seed deposition was highest at sites predominantly used by territorial males (lek and dispersed territories), compared to random sites (grasslands, shrublands and bare areas). Blackbuck territories are typically located in open habitat and territorial aggregations (leks) are largest in large open grasslands (Isvaran 2005a); consequently, our findings imply that seeds are moved from parent trees to microsites in new habitats, empty of woody plants. In contrast to territorial males, female-biased groups and bachelor males, which have larger home ranges, seem

to have little influence on the dispersal of *P. juliflora* seeds. Habitats used by these individuals had very low presence of seeds and seedlings.

Similar movement of seeds to more open sites has been described for the tree, *Trewia nudiflora* in dung depositions in grasslands by the Indian rhinoceros *Rhinoceros unicornis* (Dinerstein and Wemmer 1988). Documented evidence for within-species variation in seed dispersal patterns is relatively rare; the existing evidence has come from closed canopy tropical forests and from frugivorous birds with distinctive male mating displays. Our findings are closely aligned to the dispersal of the neotropical shade tolerant tree *Ocotea endresiana* by male bellbirds *Procnias tricarunculata*, which moved seeds away from parent plants to singing perch sites, where seedling recruitment was higher (Wenny and Levey 1998). Female bellbirds, dispersed seeds only relatively close to parent trees. Similarly, clumped distributions of seeds of small and large-seeded plant species were created by lekking males of the long-wattled umbrellabird *Cephalopterus penduliger* which moved seeds away from parent plants into leks, while females dispersed seeds more evenly across the landscape (Karubian et al. 2012). These studies and ours point to the importance of considering intraspecific variation when

Table 4. Analysis of probability of seed germination in the ex situ experiment: top candidate models (within 2 AICc units of best model) and model averaged parameter estimates with 95% CI from a GLM with binomial errors. DF = degrees of freedom. AICc = corrected Akaike information criterion. w = Akaike weight.

Candidate model syntax	DF	Log likelihood	AICc	ΔAICc	w
Dung + Light	4	−29.43	68.01	0	0.4
Dung + Ingestion + Light + Ingestion:Light	6	−27.17	68.89	0.88	0.26

Parameter	Estimate	CI lower limit	CI upper limit
(Intercept) Light (light present), Dung (dung present) and Ingestion (ingested seeds)	−0.76	−1.25	−0.27
Light (shade)	1.6	0.92	2.28
Dung (no dung)	0.58	0.17	0.99
Ingestion (not ingested)	−0.31	−0.93	0.31
Ingestion (not ingested): Light (shade)	0.8	0.06	1.55
Dung (no dung): Ingestion (not ingested)	0.2	−0.56	0.96
Dung (no dung): Light (shade)	−0.16	−0.91	0.59
Dung (no dung): Ingestion (not ingested): Light (shade)	−0.63	−2.11	0.85

investigating seed dispersal patterns. Ignoring such intraspecific variation in dispersal behavior may fail to capture the factors influencing the highly aggregated patterns in seed dispersal, such as blackbuck territories, which form a very small proportion of the landscape but contain most of the *P. juliflora* seeds.

The extreme territoriality in lekking populations adds a relatively unexplored dimension to dispersal patterns. Apart from seeds being concentrated on to dung- piles, because territories are clustered (50 males on average, during the mating peak, with a maximum of 90–100 males, Isvaran 2003), there is unusually concentrated seed arrival in a relatively small area (e.g. the main lek at Velavadar measured 80 000 m² in the peak mating season of 1995, Isvaran and Jhala 2000). While density dependent processes may result in high seed mortality at dung-piles, we found that seedling recruitment was substantially higher on dung-piles on the lek followed by dispersed territories compared with random sites in grasslands and shrublands, indicating that the local concentration of seeds created by territorial males continued into high local recruitment of *P. juliflora*. Thus, territories, particularly large territorial clusters, leks, were hotspots of successful dispersal of *P. juliflora* (Figure 5a–b).

To explore whether apart from concentrating seeds, dung-piles may represent particularly suitable germination conditions and/or seedling growth conditions, we carried out a simple ex situ germination experiment. We found no beneficial effect of dung and a negative effect of light on seed germination. It is possible that our limited light and dung treatments failed to capture the entire spectrum of in situ variation in light levels. Alternatively, other factors such as greater soil moisture due to repeated urination by territorial males and the moisture holding capacity of dung compared with soil may also influence seed recruitment. In addition, enhanced seedling growth conditions rather than germination conditions may be responsible for the greater seedling numbers on dung-piles compared with random sites in grasslands and shrublands.

Implications for patterns of invasion

Our study suggests that in open-plains lekking species, such as blackbuck, the behavior of territorial males may result in a distinct spatial pattern of invasion of grasslands by woody species. Our results clearly show that territorial males disperse seeds to open grassland sites, where seedling recruitment is also high and therefore likely aid in the spread of *P. juliflora*. Additionally, as territories are highly clustered, males may rapidly facilitate the creation of localized thickets of *P. juliflora*. Furthermore, both territorial males and females appear to avoid more closed habitats (Isvaran 2005a, 2007), a pattern demonstrated experimentally in other open-plains lekking species, such as Uganda kob *Kobus kob thomasi* (Deutsch and Weeks 1992). Therefore, as *P. juliflora* recruits on territorial grounds, there might be a shift by territorial males and visiting females to more open grassland areas, followed by *P. juliflora* seed dispersal into these new territorial grounds. Thus, we predict that the concentrated dispersal behavior of lek territorial males would result in local habitat modification followed by the movement of territorial males away from these modified habitats, a positive feedback process that would aid in the rapid conversion of grasslands into woodlands. Although blackbuck are known to feed only on the pods of *P. juliflora* and do not feed on *P. juliflora* seedlings, other factors such as trampling of seedlings by blackbuck on territorial grounds could negatively influence seedling survival and growth at territorial sites. However, given the low overlap between peak lekking and seed recruitment periods (coincident with the wet season), these effects may not be very strong. This hypothesis remains to be tested as managers currently uproot *P. juliflora* seedlings annually across the whole preserve at Velavadar, but large areas of the reserve are invaded by *P. juliflora*. Velavadar is one of the last remaining grassland reserves in India and harbours populations of several highly endangered grassland fauna. Understanding patterns of seed deposition can help narrow down the search effort to locate seedlings and develop more effective management practices (Murphy et al. 2008).

Implications for disperser ecology and behavior

The alteration of grasslands into woodland by *P. juliflora* also has implications for blackbuck behavior and population patterns. Blackbuck leks are only seen in grassland sites, and dispersed territoriality is seen in more closed habitats, such as shrublands and woodlands (Isvaran 2007). Furthermore, group sizes and local densities have also been shown to decrease as habitats become more closed (Isvaran 2005a, 2007).
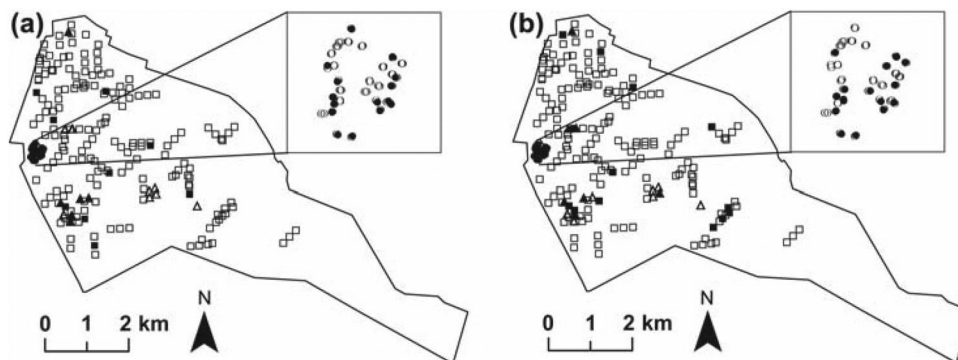

Figure 5. Map of study area, Velavadar National park, with plots on dispersed territories (triangles), lek territories (circles) and random sites (squares) with seeds (filled symbols) and without (open symbols) (a), and with seedlings (filled symbols) and without (open symbols) (b). Inset shows lek territories. For ease of viewing, the sizes of the symbols in the map are larger than the actual plot sizes.

Thus, lek territorial males, by aiding *P. juliflora* spread, could modify habitats negatively and thereby cause a mating system shift from lek territoriality to more solitary dispersed territories, a social organization shift from large herds to small groups, and a reduction in the size of blackbuck populations. Such a loss of open grassland patches, due to invasion by a number of woody species including *P. juliflora*, has been hypothesized to be the cause of the decline in the blackbuck population at Guindy National Park, India (Shankar Raman et al. 1995). The interaction between lekking blackbuck and *P. juliflora* provides a prime example of a frugivore influencing plant distribution patterns and as a consequence influencing their own behavior and populations.

It is indeed difficult to address if *P. juliflora* should be completely eradicated from the Velavadar landscape. *Prosopis juliflora* constitutes an important food source for blackbuck at Velavadar, especially during the dry season and droughts when the nutritional levels in grasses are low, particularly since the local migrations that these antelope may have undertaken during droughts in search of food and water are now not possible due to severe reductions in grassland habitat (Jhala 1997). Nevertheless, further invasion of *P. juliflora* in Velavadar is likely to have adverse effects on the blackbuck population as well as other highly endangered native species dependent on grassland habitats (e.g. lesser florican, *Sypheotides indicus*). Given the prominence of *P. juliflora* in the diet of blackbuck, we recommend that its control should be carefully conducted on an experimental basis while monitoring blackbuck populations and assessing the need for supplementary strategies.

In conclusion, our study, along with a growing number of other studies (Wenny and Levey 1998, Westcott et al. 2005, Karubian et al. 2012), highlights the importance of incorporating variation in frugivore behavior into predicting patterns of seed dispersal. Our work shows how extreme mating strategies (lek territoriality) in an animal disperser can have profound effects on seed dispersal, with a potential to influence plant distribution patterns which can feed back into the behavior and ecology of the disperser species. This phenomenon is likely to be widespread as a range of bird and animal species show mating systems in which males defend display sites and mating territories aggregated to various degrees, and are likely to show foraging and ranging patterns that are distinctly different from females and non-breeding males (Clutton-Brock 1989, Davies 1991). Finally, incorporating the existing understanding of factors influencing location of blackbuck territories (Isvaran 2005a), into our dispersal model can help predict pattern of spread of invasive *P. juliflora* into grassland habitat and guide action for management of this invasive woody plant.

Supplementary material (Appendix 1) follows the **References**.

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Appendix 1

Table A1. Analysis of variation in dung density between lek and dispersed territories (DT) and also, on versus off dung piles within a territory. Top candidate models (within 2 AICc units of best model) and model averaged parameter estimates with 95% CI (below) from GLMM with binomial errors. DF = degrees of freedom. AICc = corrected Akaike information criterion. w = Akaike weight.

Candidate model syntax	DF	Log likelihood	AICc	ΔAICc
Territory (lek/DT) + Location (on / off dung pile) + Terrritory: Location	5	−190.79	391.58	0

Parameter	Estimate	CI lower limit	CI upper limit
(Intercept) Territory (DT) and Location (off dung pile)	−5.15	−6.12	−4.18
Territory (lek)	1.92	0.833	3
Location (on dung pile)	5.5	4.7	6.29
Territory (lek)**:** Location (on dung pile)	−1.357	−2.20	−0.53

Table A2. Analysis of latency in *P. juliflora* seed germination under different treatments in the ex situ experiment. Top candidate models (within 2 AICc units of best model) and model averaged parameters and 95% CI (below) from GLM with Poisson errors. DF = degrees of freedom. AICc = corrected Akaike information criterion. w = Akaike weight.

Candidate model syntax	DF	Log likelihood	AICc	ΔAICc	w
Dung + Ingestion + Light + Ingestion: Light	6	−1056.7	2125.7	0	0.41
Dung + Ingestion + Light + Dung: Light + Ingestion: Light	7	−1056.4	2126.98	1.28	0.22
Dung + Ingestion + Light + Dung: Ingestion + Ingestion: Light	7	−1056.6	2127.46	1.76	0.17

Parameter	Estimate	CI lower limit	CI upper limit
(Intercept) Light (light), Dung (dung present) and Ingestion (ingested seeds)	3.38	3.25	3.51
Light (shade)	–0.30	–0.48	–0.13
Dung (dung absent)	–0.24	–0.30	–0.17
Ingestion (not ingested)	–0.06	–0.15	0.03
Ingestion (not ingested): Light (shade)	0.14	0.04	0.23
Dung (dung absent): Ingestion (not	0.04	-0.05	0.14

ingested)

Dung (dung absent): Light (shade)	−0.03	−0.13	0.07
Dung (dung absent): Ingestion (not ingested): Light (shade)	0.02	−0.17	0.21