ENDEMIC FARASAN GAZELLE (*GAZELLA GAZELLA FARASANI*) ENHANCES THE DISPERSAL OF INVASIVE *PROSOPIS JULIFLORA* ON FARASAN ISLANDS, SAUDI ARABIA

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RÉSUMÉ.— La gazelle endémique (Gazella gazella farasani) favorise la dispersion de l'invasive Prosopis juliflora sur les îles Farasan, Arabie Saoudite.— La dispersion d'une plante invasive Prosopis juliflora sur Farasan Kébir (région de Miharraq, Ouadi Matr) a été étudiée en relation avec l'endozoochorie par la Gazelle de Farasan (*Gazella gazella farasani*). Une expérience de germination a été réalisée afin de tester la viabilité des graines de *P. juliflora* et d'Acacia ehrenbergiana, deux espèces concurrentes. Elle a révélé que 0,0013 \pm 0,0009 graines d'Acacia par gramme de matière fécale ont germé, soit moins que pour les graines de *Prosopis* (0,0053 \pm 0,0022 graines par gramme). Les amas de fèces avec un semis de *Prosopis* (ou un jeune arbre à proximité) étaient nettement plus proches du centre supposé d'introduction de *Prosopis* (villages de Al-Qisar et Miharraq) que les amas sans *Prosopis*, ce qui suggère que les gazelles, dont le domaine vital (2,07 km² pour les femelles; 0,71 km² pour les mâles) englobe les jardins adjacents aux villages sus-mentionnés, contribuent à la dispersion de cette espèce envahissante. Au total, nos résultats suggèrent que les gazelles des îles Farasan contribuent au succès de l'invasion de *Prosopis*. Il reste toutefois encore à étudier dans quelle mesure le bétail domestique, en particulier les chèvres, contribue à la dispersion de *Prosopis* are filmination mécanique dans la zone protégée autour de Ouadi Matr.

SUMMARY.— Invasive *Prosopis juliflora* dispersal on Farasan Kebir (Miharraq area, Wadi Matr) was investigated in relation to endozoochory by Farasan Gazelle (*Gazella gazella farasani*). A germination experiment was conducted to test defecated seed viability of competing *P. juliflora* and *Acacia ehrenbergiana*. It revealed that 0.0013 ± 0.0009 *Acacia* seeds per gram of faeces germinated, while the rate of germinating *Prosopis* seeds was higher (0.0053 ± 0.0022 seeds per gram of faeces). Dung middens with a *Prosopis* seedling (or a young tree nearby) were distinctly closer to the putative centre of *Prosopis* introduction (Al-Qisar and Miharraq villages) than middens without *Prosopis*, suggesting that gazelles whose home ranges (mean size, females: 2.07 km^2 , males: 0.71 km^2) encompass the gardens edging the aforementioned villages contribute to the dispersal of this invasive species. Altogether, our results suggest that gazelles on the Farasan Islands contribute to the invasion success of *Prosopis*; it still needs to be investigated though to what extent also domestic livestock - in particular goats - contribute to *Prosopis* dispersal. Based on our present data it is recommended to reduce the number of *Prosopis* trees in the protected area around Wadi Matr by mechanical elimination.

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The successful population establishment of a species introduced into a new habitat depends (among other factors) on (*a*) whether or not (and to what extent) it is already adapted to the set of environmental factors encountered, and/or (*b*) its potential for adaptation to novel selection pressures (Smith & Knapp, 2001; Barrat-Segretain, 2005). Several ecological and life history traits thus determine the invasion success of an introduced plant species crowding out natural vegetation (Baker & Stebbins, 1965; Drake *et al.*, 1989; Williamson, 1996; Sandlund *et al.*, 1999; Child *et al.*, 2003). Hence, investigating some of the life history traits, such as growth, reproduction, germination and dispersal ecology, not only adds to our understanding of the general biology of an invasive species, but helps develop guidelines for its control (Fowler & Larson, 2004; Sakai *et al.*, 2001; Woitke & Dietz, 2002).

Prosopis juliflora (Sw.) D.C., Mimosaceae, native to Central and South America, was introduced to several deserts in tropical and subtropical regions, including Saudi Arabia, for greening of landscapes and for sand storm and desertification control (Ghazanfar, 1996; Western, 1989). *Prosopis* is highly invasive and coppices well, so that it often crowds out native vegetation (Robinson *et al.*, 2001; El-Keblawy & Al-Rawai, 2005; Shiferaw *et al.*, 2004). In the Kingdom of Saudi Arabia, the species has escaped urban and sub-urban areas; it invaded both natural and managed regions, including farmland, and has been associated with habitat degradation and loss of species diversity (Kothari & Jain, 2003). On Farasan Islands (Kebir) a major stand of *P. juliflora* was established between Miharraq road junction and Miharraq village forming a more or less continuous thicket along former gardens (Robinson *et al.*, 2001; Fig. 1).

The species is an evergreen shrub, producing flowers and fruits between March and May in inlands on the Arabian Peninsula (about 100-150 km from the coasts), and from October to May in coastal areas (Al-Rawai, 2004). Shiferaw *et al.* (2004) suggested that animals, both domestic and wild, may be important dispersal agents for seeds of *P. juliflora*. Seeds are adapted for endozoochory, i.e., dispersal after passage inside animals' digestive tracts. They are embedded in an attractive succulent nutritious fruit (described as 'reward' for the disperser; Fenner, 1985; Stiles, 1992) and are protected from the chemical and abrasive action they encounter in the gut by tough seed coats (Shiferaw *et al.*, 2004; Razanamandranto *et al.*, 2004). The hard seed coat creates a physical dormancy in *P. juliflora*, which can be broken by passing through the digestive tract of animals or – artificially – by seed pre-treatment with sulphuric acid and boiling water (Shiferaw *et al.*, 2004; Pasiecznik *et al.*, 1998).

One potential dispersal agent of *Prosopis* on the Farasan Islands is the Farasan Gazelle (*Gazella gazella farasani*, Thouless & Al-Bassri, 1991). This sub-species occurs endemically on the Farasan Archipelago (Thouless & Al-Bassri, 1991). While most Mountain Gazelle populations on the Arabian Peninsula are declining (Mallon & Kingswood, 2001), the Farasan population is still believed to number around 1,000 animals (Cunningham & Wronski, 2011), even though to date very little is known about the general ecology of gazelles on the archipelago (Habibi, 1992). Farasan Kebir Island is designated as a protected area and the gazelle population nowadays receives considerable conservation efforts since it is considered to be the last viable population of the species in Saudi Arabia (Flamand *et al.*, 1988; Dunham *et al.*, 2001; Cunningham & Wronski, 2011). Most abundant are the gazelles in the northern part of Farasan Kebir around Seir village and in the southern part west of the village of Miharraq (Cunningham & Wronski, 2011).

Robinson *et al.* (2001) reported that domestic goats, rather than gazelles, browse on *Prosopis*, while gazelles were reported to prefer leafs and pods of *Acacia ehrenbergiana*. Consequently, gazelles were assumed to contribute little to the observed spread of *Prosopis*, and domestic goats were thought of as the major dispersal agents on the Farasan Islands. If this were true, a straightforward objective for management plans trying to stop the spread of invasive *Prosopis* would be to simply keep goats out of protected areas on Farasan Kebir. There is no physical barrier between villages, former gardens and the protected area, but since the proclamation of the protected area in 1988, rangers patrol the study area at intervals of one to two hours, ensuring that goats and other domestic livestock do not penetrate the area. Therefore, goats are unlikely to contribute to *Prosopis* dispersal anymore.

In this study we hypothesized that Farasan Gazelles foster *Prosopis* dispersal. If this assumption was true, then gazelle faeces should contain at least a moderate amount of *Prosopis* seeds that are able to germinate after having passed the digestive tract. We tested this hypothesis via a germination test using gazelle faeces collected in the wild. Moreover, faeces of gazelles (and hence, probably also *Prosopis* seeds) accumulate in localized defecation sites, or dung middens, which gazelles use for intra-specific communication (Habibi, 1991; Walther *et al.*, 1983; Grau, 1974; Wronski & Plath, 2009). Animals whose home ranges (males: 0.71 km²; females: 2.07 km²) encompass a *Prosopis* thicket are obviously more likely to disperse the seeds through their dung than animals whose home ranges do not. We, therefore, also examined distribution patterns of latrines with and without *Prosopis* seedlings and predicted that dung middens containing a *Prosopis* seedling would be closer to the putative nucleus of *Prosopis* introduction (i.e., already existing *Prosopis* thickets around villages and neglected gardens) than middens without *Prosopis* seedlings.

MATERIAL AND METHODS

STUDY AREA

The Farasan Islands are an archipelago in the Red Sea formed of raised fossil coral reefs, located approximately 80 km off the coast of Jizan in the extreme south-west of Saudi Arabia (Flamand *et al.*, 1988; Child & Grainger, 1990). Although there are more than 300 islets (Anon, 2000), only the two largest - Farasan Kebir (400 km^2) and As Saqid (160 km^2) - are permanently inhabited by humans (Flamand *et al.*, 1988). Large parts of the islands are weathered flat gravel plains incised by - often well vegetated - wadis and other broken terrain formed when the fossil reef was raised by underlying salt domes (Flamand *et al.*, 1988).

The climate is arid and the annual rainfall is highly variable, ranging between 50 and 100 mm per year (Child & Grainger, 1990). There is no permanent surface water (Flamand *et al.*, 1988). Isolated thickets of *Acacia ehrenbergiana* occur on the gravel plains while the vegetation in the wadis consists of a variety of grasses, shrubs and trees including *A. ehrenbergiana, Capparis decidua* and *Commiphora gileadensis* (Flamand *et al.*, 1988). *Prosopis juliflora*, an invasive alien species, has also become established on parts of Farasan Kebir (Robinson *et al.*, 2001). Large stands are most obvious around the villages of Al Qisar and Miharraq in the southern part of the island (Fig. 1).

Our study area on Farasan Kebir covers about 14.4 km², extending east of the villages of Al Qisar and Miharraq, bordered in the north by the main road and in the south by a Pleistocene coral cliff. To the west it is confined by barren gravel plains or coastal vegetation. The area is dominated by Wadi Matr, an *Acacia* thicket of approximately 1 km², but otherwise comprised of gravel plains, small vegetated drainage lines and former gardens. These gardens edge the two villages and represent the putative nucleus of *Prosopis* intrusion on the island. Another nucleus was identified in a north-eastern garden situated in a groove with accumulated silt top soil.

THE FARASAN GAZELLE (GAZELLA GAZELLA FARASANI)

Mountain Gazelles (*G. gazella*) inhabit a wide range of habitats but prefer rocky, hilly terrain with suitable vegetation (Baharav, 1981, 1983) and avoid open sand plains and dense forest (Mendelssohn *et al.*, 1995). Several studies reported that although *G. gazella* is intermittently a grazer (Baharav, 1981, 1983; Harrison & Bates, 1991), its distribution on the Arabian Peninsula closely coincides with that of *Acacia* (Vesey-Fitzgerald, 1952; Mendelssohn *et al.*, 1995).

G. g. farasani is described as an endemic subspecies from the Farasan Archipelago (Thouless & Al Bassri, 1991; Wronski *et al.*, 2010), and may have been isolated from mainland populations since the last Ice Age (approximately 15,000 years ago). The population on Farasan Kebir nowadays numbers about 1,000 animals. Our study area on Farasan Kebir harbours around 170 to 190 gazelles, equalling approximately 3.2 animals per km² (Cunningham & Wronski, 2011). During the day gazelles in our study area rest mostly inside *Acacia* thickets (Wadi Matr) while at night they visit the gardens edging the villages to forage (Wronski, unpubl. data). Behavioural observations of Farasan Gazelles repeatedly found gazelles feeding on *P. julifora* pods (Wronski, unpubl. data).

DATA COLLECTION

During a dung midden survey (from March to July 2009), initiated to establish the function of localized defecation of Farasan Gazelles in the context of their social organization and mating system, the study area was systematically searched for dung middens. Dung middens were mapped by traversing the total study area on foot (in total 116 km) as efficiently as possible, predominantly along drainage lines, including all larger trees and as many shrubs and other landmarks as possible. Open gravel plains were sampled systematically by walking transects approximately 70 m apart. Positional data were recorded for all dung middens (n = 523) using a Garmin 12 GPS and were later processed as UTM coordinates using a geographic information system (Arcview 3.2a, ESRI).

To analyse the occurrence of *Prosopis* seeds capable of germination in gazelle faeces, we collected dry faeces (39 to 94 g) from 27 dung middens covering the fruiting seasons of both tree species [*Prosopis*: October to May (Al-Rawai,

2004); Acacia: mid May to late June (Karim & Fawzi, 2007)]. We arbitrarily sampled faeces from middens throughout the study area, including sites close to villages and gardens with dense vegetation and those on the open gravel plains. Samples in which a *Prosopis* seedling was found were taken at distances between 364 and 1760 m (mean \pm SE: 974.1 \pm 174.6 m) from the nearest garden, those without a *Prosopis* seedling at distances between 453 and 3202 m (1307.7 \pm 169.9 m). Faecal samples were stored in plastic containers and transferred to the laboratory at King Khalid Wildlife Research Centre (KKWRC). Here faeces were crashed in a plastic bowl using a commercially available hand rake and were then searched for *Prosopis* and *Acacia* seeds. To ensure proper identification, ripe pods were collected from several trees of both species at the study site, the seeds removed and sun dried. For each sample containing either *Acacia* or *Prosopis* seeds (or both), we divided the number of seeds by the total mass of that sample to establish the seed density.

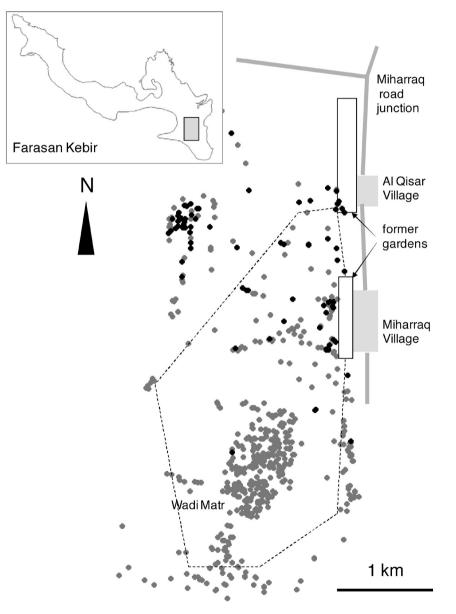


Figure 1.— Schematic map of the study area showing the distribution of gazelle dung middens with a *Prosopis* seedling or young tree (black) and those without (grey). The dotted line indicates the extension of a female group home range as determined by Wronski *et al.* (unpubl. data). The positions of two putative nuclei of introduction and high *Prosopis* density (i.e. former gardens at Miharraq and Al-Qisar village) are indicated. The inlet shows the location of the study area on Farasan Kebir.

After the seeds were extracted from the faeces, all intact seeds were selected for a germination tests. These were sown in 5.5 cm petri dishes on moistened cotton wool, placed in the laboratory at KKWRC with sun light entering the room through several windows. Seeds were considered to have germinated when the radicle penetrated the seed coat. Germinating seeds were counted every other day and removed from the dishes. All seeds were incubated for a maximum of 14 days, after which the germination status of all seeds was assessed and the test terminated (Baskin & Baskin, 1989).

DATA ANALYSIS

We used a non-parametric Wicoxon Signed Rank test to test for differences between overall *Acacia* and *Prosopis* (1) seed density in gazelle faeces (numbers of seeds per gram of faeces) and (2) densities of germinating seeds of both plant species.

We further predicted that middens with a young *Prosopis* tree next to it (< 30 cm distance), or a *Prosopis* seedling growing inside the midden, should be closer to the putative nucleus of introduction than dung middens without. Hence, Mann-Whitney U tests were used to compare distances to the nearest putative nucleus of introduction for both categories of dung middens.

RESULTS

GERMINATION SUCCESS OF PROSOPIS AND ACACIA SEEDS IN GAZELLE FAECES

A total of 1.84 kg (39 to 94 g per sample; n = 27 samples) of gazelle faeces was analysed. In total, we detected four *Acacia* seeds and 21 *Prosopis* seeds. The mean (± SE) *Acacia* seed density in gazelle faeces obtained from dung middens was, therefore, determined as 0.002 ± 0.001 seeds per gram faeces, that of *Prosopis* seeds as 0.015 ± 0.007 seeds per gram faeces. This difference bordered significance (Wicoxon signed rank test: W = 55, T = 25, N = 28, P = 0.09).

Out of the four *Acacia* seeds, two seeds germinated, while out the 21 *Prosopis* seeds only eight germinated. Accordingly, the mean (\pm SE) density of germinated *Acacia* seeds per gram faeces was calculated as 0.0013 ± 0.0009 , while that of germinated *Prosopis* seeds was 0.0053 ± 0.0022 seeds per gram faeces, but - as for seed density in general - there was no significant difference between densities of germinated *Acacia* and *Prosopis* seeds (Wicoxon signed rank test: W = 30, T = 6, N = 28, P = 0.11), suggesting that gazelles in our study area contribute to the dispersal of both species, with a slight bias in favour of *Prosopis*.

DISTRIBUTION PATTERNS OF DUNG MIDDENS WITH OR WITHOUT PROSOPIS SEEDLINGS

Most middens containing a *Prosopis* seedling were approximately 20 to 200 m from the putative introduction nucleus, while most of those without a *Prosopis* tree or seedling were located between 1000 and 2200 m from the nucleus. The mean (\pm SE) distance between dung middens containing *Prosopis* seedlings (or young trees) and the nearest putative nucleus of introduction was only 419.9 \pm 42.7 m while in the case of dung middens without *Prosopis* the distance to the nearest putative nucleus of introduction was 1579.9 \pm 37.1 m (Fig. 2). This difference was statistically significant (Mann-Whitney *U* test: *T* = 5,543, *N* with *Prosopis* = 71, *N* no *Prosopis* = 452, *P* < 0.001).

DISCUSSION

Our results confirmed the presence of both *Acacia* and *Prosopis* seeds in the dung of Farasan Gazelles. One measure of the effectiveness of an animal as an agent of seed dispersal (via endozoochory) is the number of plant species whose seeds are normally found in a viable state in the dung (Fenner, 1985). Indeed, apart from viable *Acacia* and *Prosopis* seeds, seeds from a number of other species were found in the dung of Farasan Gazelles. With a mean of 21.17 seeds per kg of faeces (all plant species combined, including undetermined species), however, our results are far below values reported from droppings of elephants in Tanzania (Lamprey *et al.*, 1974), free-living baboons in Ghana (Liberman *et al.*, 1979), or cattle (Mekuria *et al.*, 1999), warthogs, and goats in the Ethiopian Rift Valley (Shiferaw *et al.*, 2004).

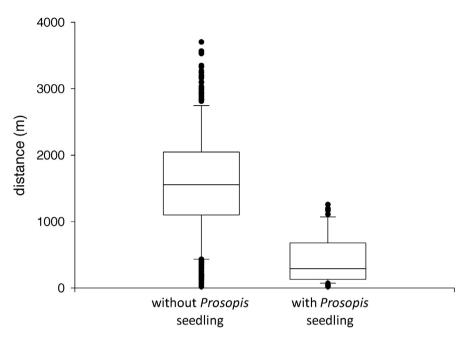


Figure 2.— Distances of dung middens with and without *Prosopis juliflora* seedling to the nearest garden (putative centre of introduction) in the study area on Farasan Kebir. Box plots showing the median (middle line), the interquartile range (box), the 5th/95th percentiles (whiskers) and outliers (bold circles).

In our germination experiment, only a relatively small proportion of seeds germinated. The remaining seeds probably stayed dormant and in nature would form soil seed banks (Shiferaw *et al.*, 2004). Although results from the germination experiment revealed that relatively few seeds (38 %) of *Prosopis* germinated, while germination was higher for *Acacia* (50 %), the absolute germination rate (per gram of faeces) tended to be lower in *Acacia* than in *Prosopis*, which was probably due to the higher overall number of *Prosopis* seeds in gazelle faeces. *Prosopis* seeds are embedded in an attractive succulent nutritious fruit, technically known as 'reward' (for the disperser). Pods of *Prosopis* have high sugar content, are low in antifeedants, and are widely sought after by a variety of animals.

Animals, both domestic and wild, are very important dispersal agents of seeds of many plants. Among the various types of dispersal facilitated by animals, a large proportion of plant species have seeds that are adapted for endozoochory (Fenner, 1985; Stiles, 1992). Endozoochory of its seeds offers *Prosopis* triple advantages in that: (1) the seeds are dispersed with the facees at some distance from the parent plant; (2) seeds that pass through the gut of animals are exposed to some treatments that facilitate germination, and (3) the facees themselves may act as fertilizer in the initial, mostly critical, stage of establishment of the seedlings. Thus, adaptation of *Prosopis* seeds to endozoochory, as demonstrated by Shiferaw *et al.* (2004), can be thought of as one of the factors enhancing its rampant invasion in the study site and zoochory can be viewed as the principal driver for shrub species encroachment on Farasan Islands.

Our results further suggest that *Prosopis* dispersal in the study area west of Al-Qisar and Miharraq village is closely related to preferred feeding sites of gazelles and their home ranges as determined by Wronski *et al.* (unpubl. data). Distances of dung middens with a *Prosopis* seedling or young tree were found to be closer to putative *Prosopis* introduction sites (i.e. gardens and villages) than middens without *Prosopis*. Hence, our present study suggests that indigenous Farasan Gazelles likely contributed to the dispersal of *Prosopis* (and *Acacia*) seeds on Farasan Kebir. However, areas closer to the putative nucleus of introduction also have more seed banks that may (partly) germinate even without passing the gut of animals, contributing -

beside high foraging and defecation activities of the gazelle - to the highest densities of *Prosopis* in the gardens and villages. Seeds from such latent seed banks may get dispersed by floods during or after peak rainfall events (Pasiecznik *et al.*, 2001).

Successful regeneration or invasion by a plant species depends upon its seeds being dispersed to suitable sites/conditions (technically known as 'safe sites'; Harper, 1977), where they can germinate and establish seedlings (Fenner, 1985; Willson, 1992). The patchy upcoming of *Prosopis* in the Miharraq area seems to be attributable to the dispersal mode of its seeds, i.e. the concentrated deposition of seeds by gazelles in 'seed shadows' (dung middens). The high density of *Prosopis* individuals (trees and seedlings) in the putative introduction site (i.e. gardens of Al Qisar and Miharraq village) but also in Wadi Matr, may be attributable, in part, to the higher ground water level in these areas. In the United Arab Emirates it has been documented that the distribution of *P. juliflora* correlates with a higher groundwater table (Al-Rawai, 2004).

CONCLUSIONS AND RECOMMENDATIONS

Our study provides evidence that Farasan Gazelles indeed contribute to the enhancement of *Prosopis* on the archipelago. This contradicts earlier reports which stated that mainly (or exclusively) goats browse on the rewarding fruits of *Prosopis*. Although it was shown that Farasan Gazelles consume *Prosopis* pods and disperse seeds, it has not yet been clarified to what extent also domestic goats contribute to dispersal. Nevertheless, ranger reports ensure that goats nowadays browse only in the gardens next to the villages and goats penetrate the study area only occasionally. It is, therefore, highly unlikely that goats are responsible for the *Prosopis* dispersal several hundred meters away from the gardens. However, future studies on Farasan Kebir should address this question in more detail and include faecal samples from goats browsing close to the study area.

In general, it appears that *Prosopis* can grow in a wider spectrum of ecological and climatic conditions and better resist unfavourable conditions through their hard seed coats (and other strategies) than many indigenous species such as *Acacia*. *Prosopis* therefore benefits disproportionally more from the dispersal by gazelles than the indigenous *Acacia ehrenbergiana* and may sooner or later outcompete *Acacia* on the island. *Prosopis* invasion thus poses a severe risk to the indigenous flora and should be addressed as soon as possible. Focus should be on the new young stands of *Prosopis* coming up afar from villages and gardens (especially in dung middens). A long-term objective should be the total eradication of *Prosopis* in the study area and possibly in the villages and gardens. KKWRC has developed strategies to tackle this enterprise and would be in the position to implement a *Prosopis* eradication program on Farasan Islands if funding is available.

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