Oecologia (2011) 167:97–105
DOI 10.1007/s00442-011-1964-6

PLANT-ANIMAL INTERACTIONS - ORIGINAL PAPER

Interaction between ungulates and bruchid beetles and its effect on *Acacia* trees: modeling the costs and benefits of seed dispersal to plant demography

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Received: 2 November 2009 / Accepted: 3 March 2011 / Published online: 27 March 2011
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Abstract Integrative studies of plant–animal interactions that incorporate the multiple effects of interactions are important for discerning the importance of each factor within the population dynamics of a plant species. The low regeneration capacity of many *Acacia* species in arid savannas is a consequence of a combination of reduction in seed dispersal and high seed predation. Here we studied how ungulates (acting as both seed dispersers and herbivores) and bruchid beetles (post-dispersal seed predators) modulate the population dynamics of *A. raddiana*, a keystone species in the Middle East. We developed two simulation models of plant demography: the first included seed ingestion by ungulates and seed predation by bruchids, whereas the second model additionally incorporated herbivory by ungulates. We also included the interacting effects of seed removal and body mass, because larger ungulates destroy proportionally fewer seeds and enhance seed germination. Simulations showed that the negative effect of seed predation on acacia population size was compensated for by the positive effect of seed ingestion at 50 and 30% seed removal under scenarios with and without herbivory, respectively. Smaller ungulates (e.g., <35 kg) must necessarily remove tenfold more seeds than larger ungulates (e.g., >250 kg) to compensate for the negative effect of seed predation. Seedling proportion increased with seed removal in the model with herbivory. Managing and restoring acacia seed dispersers is key to conserving acacia populations, because low-to-medium seed removal could quickly restore their regeneration capacity.

Keywords Herbivory · Population growth rate · Seed removal · Seed predation · Simulation models

Introduction

Plant regeneration is a complex process which encompasses a series of linked stages (Clark et al. 1999), many of them mediated by plant–animal interactions (Herrera and Pellmyr 2002). Many such studies focus on the early consequences of plant–animal interactions (i.e., those affecting seedling recruitment), but there are relatively few that emphasize the importance of those interactions in plant demography (Wang and Smith 2002; Brodie et al. 2009). In the vast literature on seed dispersal, for instance, there is a need for studies examining the plant–disperser interaction

Communicated by John Silander.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-011-1964-6) contains supplementary material, which is available to authorized users.

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within the context of plant population dynamics (Howe and Miriti 2004; Godínez-Álvarez and Jordano 2007).

One of the main interests in studying the ecological dynamics of species interactions is to understand them within the context of their costs and benefits (Bronstein 2001). In principle, any interaction lies within a dynamic position along a continuum of positive vs. negative effects. Well-studied examples of a conflict of interest between plant–animal interactions (Herrera and Pellmyr 2002) are: (a) pollination by insects whose larvae feed on developing seeds (e.g., the yucca, senita cactus and the globeflower), (b) ant-guarding conflict with pollination and plant defence (i.e., mostly in acacia trees), and (c) between seed predation and dispersal of scatter hoarders. Mammal herbivores have traditionally been studied from the point of view of their negative effect on vegetation (e.g., grazing, browsing), but there is not much evidence for their positive effects (i.e., during the seed dispersal process; Bodmer and Ward 2006). In African and Middle Eastern savannas, many plant species are exclusively adapted to be consumed by mammalian herbivores (e.g., those with indehiscent fruits and hard seed coats), and thus their presence could have strong positive effects on plant regeneration (Bodmer and Ward 2006).

We also know that the net effect of a given interaction on plant success depends not only on its strength (i.e., weak vs. strong) and direction (i.e., positive vs. negative), but also on the interrelationships between the other interactions and how they affect the plant's life cycle (Ehrlén 2002). In the tropics and subtropics, for instance, interactions between plants, vertebrate dispersers, and invertebrate seed predators are fairly common and seem to strongly determine the regeneration of many plant species (Silvius and Fragoso 2002; Bravo 2008) as well as the diversity and structure of plant communities (Wills et al. 1997). Thus, integrative studies—that is, those incorporating the multiple effects of interactions—allow one to discern the importance of each of them on the plant's life cycle (Ehrlén 2002).

Many tropical frugivores are at risk of extinction from habitat loss and fragmentation (Cordeiro and Howe 2001), as well as overhunting (Peres 2000; Peres and Palacios 2007). Under such circumstances, plant regeneration is directly related to the seed dispersal service, and thus the abundance or density of the seed dispersers determines the population dynamics of the dispersed plant. In arid savannas of the Middle East, acacia species are threatened in many areas due to high mortality and low regeneration capacity (Rohner and Ward 1999). Direct human disturbance (e.g., lowering of ground-water levels due to agriculture and road construction) may have increased acacia mortality (Ward and Rohner 1997), but the low regeneration seems to be mainly caused by a combination of reduced seed dispersal (due to local extinction of ungulates, their main seed dispersers) and high seed predation by bruchid beetles (Rohner and Ward 1999). These two processes are interlinked by the complex interaction between ungulates and bruchids, which seem to affect the entire acacia life cycle (Rohner and Ward 1999; Or and Ward 2003; Bodmer and Ward 2006). The positive effect of ungulates on seed ingestion and recruitment may, however, be counterbalanced by their negative effects through direct herbivory. Despite the complexity of plant–animal interactions in the acacia life cycle, most stages have been studied separately (but see Rohner and Ward 1999), and we are only beginning to understand how the different components interact and affect acacia population dynamics.

To investigate how ungulates and bruchids modulate the population dynamics of *Acacia raddiana*, we have developed simulation models that combine the different stages of the plant's life cycle and the interactions between plants, ungulates, and bruchids. We present the results of two different models for *A. raddiana* based on previously published data in the Negev desert (Israel; Rohner and Ward 1999). The first includes the effects of seed ingestion (over a range of ungulate body masses) and seed predation on acacia population dynamics. The second model adds browsing by ungulates to these effects with the purpose of exploring the trade-off between their positive and negative effects on acacia population dynamics. The specific questions we address are: (1) what abundance of ungulates (as a *proxy* for seed removal and browsing intensity by ungulates) enhances seed germination and compensates for the joint negative effects of herbivory and seed predation, and (2) which group of ungulates (measured in terms of body mass) has potentially the largest impact on acacia population dynamics?

Materials and methods

Study system

Acacia raddiana is a tree distributed in North Africa (from Senegal eastward to Somalia) and the Middle East (western Arabian Peninsula). This species, occurring at altitudes up to 1,600 m a.s.l., is widespread in arid and semi-arid savannas, mostly on river terraces and ephemeral river courses. Fruits are indehiscent pods, holding up to ten seeds. Ripe pods are released to the ground from June to July, accumulating beneath the parent plant. Seeds remain in pods until they are eaten, trodden on, or degraded by fungal attack (Ashkenazi 1995). Germination takes place in autumn, usually after heavy rains. In general, there is little seedling establishment due to low seed germination rates and high seedling mortality by drought. In the case of the

Negev desert, for example, suitable conditions for germination occur every 3–4 years (Ashkenazi 1995). According to a semi-stochastic model, approximately two mast events of highly successful recruitment per century combined with a low annual probability of recruitment events are necessary to sustain *A. raddiana* populations in the Negev desert (Wiegand et al. 2004). Maximum adult survival is about 50 years (Ward and Rohner 1997).

Acacia pods are widely consumed by ungulates (Bodmer and Ward 2006), due to their high protein content (i.e., ~35%). *Acacia raddiana* pods are no exception, and they are dispersed by many species of ungulates (Halevy 1974), such as Dorcas gazelles (*Gazella dorcas* L.), Nubian ibex (*Capra ibex nubiana* F. Cuvier), and the domestic goats (*Capra hircus*) and camels (*Camelus dromedarius* L.) of the Bedouin people in the Negev desert (Halevy 1974; Rohner and Ward 1999). Noningested seeds of *A. raddiana* germinate at very low rates (usually lower than 5%). Seed ingestion greatly improves germination (Or and Ward 2003), although at the cost of increased seed mortality. In the case of *A. raddiana* and *A. tortilis*, furthermore, seed germination is positively correlated with the body mass of ruminant ungulates, probably because retention time (and, hence, abrasion of the seed coat) increases with body mass (Bodmer and Ward 2006; Clauss et al. 2007; Ward 2009). A high percentage (up to 99%) of ingested seeds of *Acacia* spp. may be destroyed (i.e., chewed and/or digested) when consumed (Miller 1995; Rohner and Ward 1999; Or and Ward 2003), reducing the seed viability and therefore the capacity for plant regeneration (Halevy 1974; Coe and Coe 1987; Miller 1995).

A. raddiana is also subject to intense seed predation by bruchid beetles (Or and Ward 2003). In general, seed infestation is low (~10%) when few pods have ripened, but it reaches up to 95% later in the season, due to seed reinfestation by new generations of bruchids (Rohner and Ward 1999). Seed germination of infested seeds is usually very low (about 1–5%; Or and Ward 2003), and depends on the proportion of cotyledons and embryos eaten by the larvae (Lamprey et al. 1974). Bruchids can also infest seeds while pods are still green on acacia trees (Rohner and Ward 1999). Nevertheless, infestation rates tend to be lower in seeds ingested and defecated by ungulates (Or and Ward 2003). As a consequence, seed infestation seems to occur primarily before dispersal and is very sensitive to removal rates (which, in turn, should be positively correlated with ungulate abundance). The relationship between removal rate and seed infestation may range between two extremes documented by previous observations. At one extreme, seed removal is low when ungulates are absent or present at very low densities (e.g., in the Negev desert) and adult beetles emerge (and may lay eggs in uninfested seeds) before fruits are eaten (Lamprey et al. 1974; Rohner and Ward 1999). At the other extreme, seed removal is high under high ungulate densities (e.g., in the Serengeti, East Africa) and result in the rapid consumption of acacia fruits, so that bruchids are killed at early larval stages when passing through the digestive tract of ungulates (Lamprey et al. 1974).

Apart from pods, green leaves of acacia are also an important food and water source for ungulates, especially in the dry season. In arid savannas, the grass layer lasts for very short periods of the year, so acacia trees are a reliable food source for many savanna ungulates due to the high protein contents of foliage and pods (Owen-Smith 1988). For instance, the diet of Nubian ibex comprises 68% acacia leaves in the Dead Sea area (Hakham and Ritte 1993), and *A. raddiana* and *A. tortilis* represent 87 and 58% of the food of *Gazella gazella* and *G. dorcas*, respectively, in the southern Arava (Negev desert; Ashkenazi 1995 and references therein).

The models

The main aim of the present work was to study the importance of ungulates as dispersal agents and how they affect the regeneration of *A. raddiana*, because seedling emergence and survival are key factors in their population dynamics (Wiegand et al. 1999). Wiegand et al. (1999, 2000a, b) developed a spatially explicit individual-based simulation model, SAM, to better understand the population dynamics of acacia trees, and they found that there has been episodic recruitment for many decades (Wiegand et al. 2000b). Wiegand et al. (1999) conducted sensitivity analyses of model parameters and assumptions and found that an increase in the germination rate of acacia seeds, such as may result from passage through the digestive tract of large mammalian herbivores, was capable of counteracting the detrimental effect of unfavorable climatic conditions. The present model was based on the population models presented by Wiegand et al. (2004), since this was considered to be the most realistic scenario for seedling recruitment for *A. raddiana* in the Negev desert. Under different scenarios of offspring and survival rate, the previous authors tested the minimum number of recruitment events necessary to sustain acacia populations. Wiegand et al. (2004) developed three models to estimate the frequency of recruitment necessary for long-term population survival; two models (i.e., one deterministic and one stochastic) assumed purely episodic recruitment, whereas the third semi-stochastic model simulated a mixture of continuous and episodic recruitment (i.e., a constant rate of seedling recruitment was mixed with mast events of highly successful recruitment). The model presented here was based on the semi-stochastic population model presented by Wiegand et al. (2004), but here we explicitly incorporate the net effect of the interactions between bruchids and ungulates on the population dynamics of *A. raddiana*.

Common considerations that apply to this and the model published by Wiegand et al. (2004) are that: (1) the seed production of breeding *A. raddiana* is a function of tree size (Wiegand et al. 1999; Ward 2009); (2) the (negative) effect of mistletoe infestation (4% of trees) on seed production was low and independent of tree size (Wiegand et al. 1999); (3) the proportion of trees that produce seeds in a given year is above 80% (except for very small trees; Wiegand et al. 1999); (4) a high proportion of seeds (i.e., 93%) is lost due to transport by floods and ungulates outside ephemeral river beds (Wiegand et al. 1999); (5) seedling survival was set to 10%, which depends on the proportion of good, intermediate and poor rainfall years (Wiegand et al. 1999; Wiegand et al. 2004); (6) to avoid unrealistically high densities, we restricted the number of recruits per recruitment event to 5,000, and; (7) we assumed an age-independent survival of older acacia plants. For further details on the life history of *A. raddiana* in the Negev, see Ward and Rohner (1997), Rohner and Ward (1999), and Wiegand et al. (1999, 2000a, b). For further information about model construction, see Electronic supplementary material (ESM) 1.

Our model considered the "fertility factor" (FF), which is the number of seedlings a tree of a given age produces after considering the effect of mistletoe infestation, seed transport outside river beds, and seed survival of only those seedlings that survive for 5 years (see ESM 1). The number of offspring of each tree (*O*) was calculated based on a linear relationship with the FF for each combination of seed removal and body mass of ungulates (for the definition, see below) and the plant age-class (*T*) measured in time steps of 5 years (ESM 1). We present two simulation models here, focusing respectively on (a) seed ingestion only by ungulates and (b) seed ingestion and herbivory by ungulates. Both models included seed predation by bruchids based on seed removal. For a diagram of the factors affecting *A. raddiana* regeneration that are included in the two models, see Fig. 1.

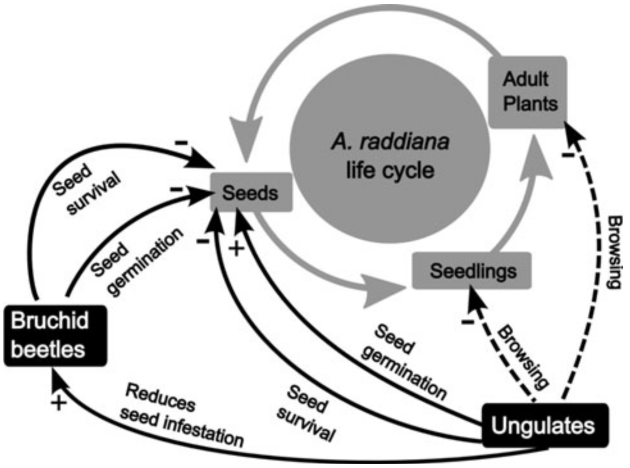

Fig. 1 Diagram showing the factors affecting *A. raddiana* regeneration in the models without (*black solid lines*) and with herbivory (*black solid plus dashed lines*). Plant life stages (*light gray boxes* and *arrows*) are affected by plant–animal interactions (i.e., bruchid beetles and ungulates; *black boxes*), which can have positive (i.e., *arrows* with "+" sign) and negative effects (i.e., *arrows* with "−" sign) on plant fitness. Those factors affecting the seed stage and seedling survival (i.e., the number of offspring that a tree of a given age produces) were defined as the "fertility factor" in the analyses (see ESM 1 and 3)

Model without herbivory

A simplified assumption of the present model was that the FF depends on seed removal by ungulates because it reduces the infestation by bruchids as they disperse seeds before they can be infested (Lamprey et al. 1974; Miller 1994). More specifically, we assumed that the proportion of ungulate-ingested seeds (and not infested by bruchids) increased with seed removal. In the present model, we defined "seed removal" as a *proxy* of ungulate abundance, affecting the relative proportion of seed groups (i.e., infested by bruchids, ingested by ungulates and intact) at increasing pressures of ungulate abundance (ESM 2). For instance, low seed removal (i.e., which occurs in the Negev desert) caused most seeds to be infested, whereas high removal of seeds (i.e., which occurs in East Africa) resulted in ungulate-ingested seeds being the most abundant seed group. In addition, the FF of acacia was also affected in two ways by the body mass of ungulates: destruction and improved germination of seeds (Miller 1995; Rohner and Ward 1999). For the present model, we used the linear relationship between the proportion of seeds surviving gut passage and ungulate body mass (Miller 1995). These data are also recorded in Bodmer and Ward (2006) for a wide range of *Acacia* species. We also used the correlation between seed germination and ungulate body mass (Rohner and Ward 1999). For more information, see ESM 1.

Consequently, the FF was calculated as a function of two variables only (i.e., seed removal and body mass of ungulates), which, in combination, affected the infestation, destruction and germination of acacia seeds (ESM 3). FF was assumed to be independent of further parameters relating to ungulates for two reasons: (a) there is no evidence that ungulates deposit seeds in microhabitats that are more suitable for seedling establishment (Ward, pers. obs.), and (b) floods produce secondary seed dispersal in this species (Rohner and Ward 1997) and other *Acacia* species (Hauser 1994). Thus, the initial pattern of seed deposition by ungulates (and, consequently its seedling fate) may be altered after secondary seed dispersal by water.

Furthermore, we also considered that there is no predation of ingested seeds because seed predators were less likely to detect scattered seeds (i.e., seeds not concentrated under fruiting plants) and locate seeds within a disperser's dung (Fragoso et al. 2003; Rios and Pacheco 2006).

Model with herbivory

This model incorporates the effects of both seed ingestion and browsing by ungulates. All relationships described in the previous model were also included here, but the herbivory model included additional terms for the intensity of browsing and its effect on reproduction (ESM 1). There are no data available that relate ungulate preference to browsing intensity of *A. raddiana*, and thus we used information from a close relative, *A. tortilis* (ESM 1). For our model, up to 25% of the acacia canopy may be browsed in conditions of maximum ungulate abundance (Fornara and Du Toit 2008a). We also assumed that browsing intensity and seed removal were two mutually related factors, since they depend on ungulate abundance (see ESM 1). We did not consider the possibility that browsing intensity is related to plant mortality (ESM 1).

The proportion of foliage browsed by ungulates (hereafter *FBU*) depended on the height of each age class of acacia and the maximum height at which ungulates were able to feed (see ESM 1). In our model, plant growth for each time step was reduced according to the proportion of *FBU*, which increased with ungulate body mass because larger ungulates could reach higher foliage (see ESM 1). Putting all effects together, smaller plants may be browsed by most ungulates, but taller plants may be accessible to the largest (i.e., heaviest) ungulates only. Herbivory also has negative costs on reproduction in acacia species. That is, highly browsed plants produce fewer fruits than unbrowsed plants (Goheen et al. 2007; Fornara and Du Toit 2008b), which may be a consequence of resource depletion and/or flower browsing. For our model, we reduced the fruit production of breeding plants (i.e., the number of fruits a tree of a given age produces after removing the effect of mistletoe infestation, see above) on the basis of the same proportion of *FBU* (see ESM 1).

Finally, we constructed 100 scenarios representing a combination of abundance and body mass of ungulates: (a) ten scenarios representing an increase of 10% in seed removal, and (b) ten scenarios representing the range of body masses of those ungulates which disperse *A. raddiana* seeds in the Negev desert [i.e., from Dorcas gazelle ($\sim$25 kg) to camel ($\sim$800 kg)]; body masses were divided into ten logarithmic mass-spans. Each two-way combination included only a single mass-span of body masses, so we did not consider the mixed effect of different seed removals and body masses of ungulates. Finally, we created one scenario without seed ingestion by ungulates (i.e., only seed predation by bruchids). Each simulation in a given scenario consisted of 100 time steps replicated in 200 runs. Each run was initialized with 1,000 trees distributed randomly among age classes using a negative exponential distribution (due to age-independent mortality; Wiegand et al. 2000b). The output variables in simulations were (a) the number and (b) the size of plants for each age-class, and (c) the population growth rate. We defined three age-class categories: seedlings ($\leq$1 time steps), subadults (i.e., $\leq$5 time steps), and adults ($\geq$6 time steps). Adult and subadults could produce fruits (Wiegand et al. 2004). For each simulation, we calculated the population growth rate. Because we were specifically interested in testing whether seed removal increased acacia regeneration capacity, we also calculated the "seedling abundance" as the ratio between the number of plants included in the seedling age-class category divided by the total number of individuals (i.e., summing all of the categories). We did not consider it necessary to perform sensitivity analyses for the variables entered in the present model, since the main determinants of the of the model sensitivity were recorded previously (Wiegand et al. 1999, 2000a, b).

Results

Simulations without herbivory showed that seed ingestion by ungulates compensated quickly for the negative effect of seed predation by bruchids. In general, seed removal >30% was enough to stabilize or increase population size (Fig. 2a). As expected, acacia population size increased more quickly with seed removal by heavier ungulates (Fig. 2a). For the largest body mass (i.e., 800 kg), acacia population size increased about 15-fold faster than for the smallest body mass (i.e., 20 kg) because of the exponential relationship between germination and body mass (Bodmer and Ward 2006; Ward 2009). Simulations also showed that the proportion of seedlings oscillated around 10% and was independent of the seed removal and body mass of ungulates (Fig. 2c).

When we included herbivory, acacia population size was reduced, on average, by 40% compared to simulations without herbivory (Fig. 2b). At seed removal $\geq$50%, the effect of seed ingestion by ungulates compensated for the seed loss produced by seed predation (i.e., acacia population size achieved the initial population size; Fig. 2b). Compared to the model without herbivory, we found the same differences between ungulate body masses; i.e., the plant population size increased about 15-fold faster with the largest than with the smallest body mass. At maximum seed removal, the heaviest ungulate had a negative effect on the acacia population dynamics because it browsed a

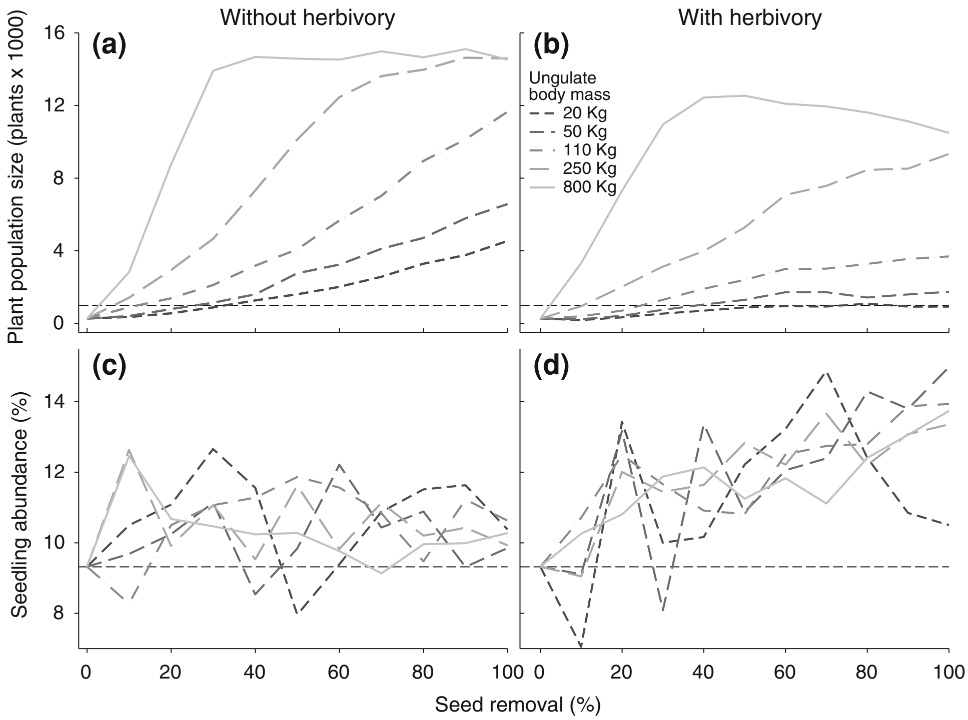

Fig. 2 Projected plant population size (**a**, **b**) and percentage of seedling abundance (**c**, **d**) in relation to seed removal modeled without (**b**, **d**) and with (**a**, **c**) herbivory by ungulates of different body mass. *Lines* represent the average of 200 simulations after 100 time steps. The *dashed lines* in **a** and **b** indicate the initial population size in units of 1,000 trees; in **c** and **d**, the *dashed lines* indicate initial seedling abundance in the scenario without seed removal (i.e., 0% seed removal by ungulates and 96.5% of infested seeds; see ESM 2), compared with other life stages. In the model with herbivory, plant browsing was proportional to seed removal (see ESM 1). For clarity of representation, only five body masses of ungulates are plotted, and standard deviations are omitted

higher percentage of plants; the population size was reduced by about 15% when seed removal was ~50% (Fig. 2b). Including herbivory, population growth rate was proportionally more reduced when small-to-medium size ungulates (i.e., from 25 to 175 kg) increased the proportion of seeds removed (Fig. 3), probably because the positive effect of seed ingestion by ungulates did not compensate for the negative effect of herbivory. Even though the seedling proportion was independent of ungulate body mass, this proportion increased with seed removal (Fig. 2d). Compared to the model without herbivory, the seedling proportion was significantly higher in the model with herbivory at seed removal $\geq$50% (paired t test between the models with and without herbivory: $t = -3.60$, $d.f. = 9$, $p = 0.006$).

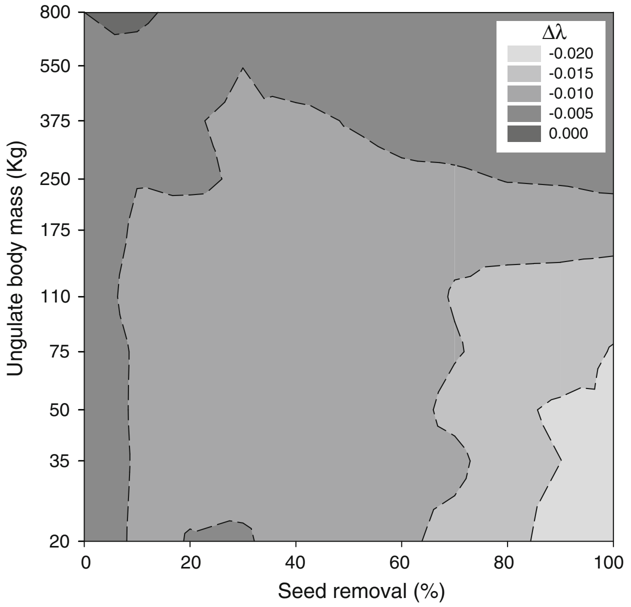

Fig. 3 Estimated change in population growth rate ($\Delta\lambda$) for *A. raddiana* in response to variations in seed removal and body mass of ungulates. $\Delta\lambda$ is the difference between λ estimated from models with and without herbivory. For $\Delta\lambda < 0$, λ was lower in the model with herbivory than in the model without herbivory, so herbivory had proportionally more negative effects on acacia population dynamics

Discussion

Even though single interaction studies are fundamental to our understanding of the ecology of particular plant–animal systems, integrative studies (i.e., those incorporating the effect of multiple interactions) are especially useful for gauging the importance of each interaction to the plant's life cycle (Ehrlén 2002). Our system is an excellent example of such an approach; it can be used to test the importance of plant–animal interactions and their effect on plant regeneration for two reasons: first, there is a trade-off between seed removal by ungulates and seed predation by bruchids, and second, ungulates impact both positively (i.e., seed removal) and negatively (i.e., herbivory, seed destruction) on the acacia life cycle (Fig. 1). Thus, our study tries to assess the relative effectiveness of each plant–animal interaction and how it affects (using the same currency) acacia population dynamics. We showed here that there was a potentially positive effect of ungulates on acacia population dynamics, even though they destroy large numbers of seeds (Miller 1995; Rohner and Ward 1999) and reduce the fruit production capacity through browsing (Goheen et al. 2007). The positive effect of ungulates arises mostly from a reduction in seed predation and an increase in seed germination (Ward 2009 and references therein). We also detected that the removal of only 10–50% of seeds by ungulates was sufficient to compensate for the negative effect of seed predation by bruchids, and to stabilize the population growth rate of *A. raddiana*. Although our model results were not validated with field data, field observations are in agreement with the results of our model with herbivory, although only at medium-to-high seed removal by ungulates—probably because excessive browsing maintains acacia regeneration, but at the cost of reducing plant growth (Reid and Ellis 1995; Rohner and Ward 1999). For example, there are relatively higher proportions of seedlings and juveniles at sites with ungulates than at sites where ungulates were excluded or present at low densities (Reid and Ellis 1995; Oba 1998; Rohner and Ward 1999; Bond and Loffell 2001).

Distinguishing the relative costs and benefits of each interaction is important in order to understand them within the perspective of ecological dynamics (Bronstein 2001). Post-dispersal seed predators destroy a large quantity of seeds, but a significant number of seeds can also be secondarily dispersed to appropriate places for establishment (Vander Wall and Longland 2004). Despite the fact that the majority of such studies are performed in the early stages of plant regeneration, it is likely that the negative effect of such seed predators could be diluted in the long term. In our case, we found that the positive effects of removal and the ingestion of seeds by ungulates are undoubtedly more important than their negative effects caused by browsing and seed destruction. Empirical studies have shown that browsing may have both positive and negative effects on plant growth, depending on whether ungulate abundance is low or high, respectively (Cowling et al. 1997 and references therein). In our model, we assumed that there is no regrowth effect on *A. raddiana* with ungulate browsing (Ward 2010), as has also been reported in many studies of herbivory on acacia growth (Du Toit et al. 1990; Oba 1998; Rohner and Ward 1999; Rooke et al. 2004). Furthermore, we also assumed no increase in plant mortality with browsing pressure (Rohner and Ward 1999); this is reasonable because of high physical (Smit 1999) and chemical defences in *A. raddiana* (Smit 1999) compared to other acacia species (Rohner and Ward 1997). In consequence, our results showed that the positive effects of seed ingestion outweighed the negative effects of herbivory on this acacia's life cycle. Under situations in which ungulates have negative effects on the growth and survival of adult plants (Bond and Loffell 2001), it is likely that the positive effect of ungulate presence could peak at low-to-medium seed removal due to high ungulate abundance results in negative effects on seed growth and plant survival.

Plant–disperser systems are excellent cases for comparing the relative effectiveness of different mutualist partners, because dispersers usually differ in both dispersal quantity and quality (Schupp et al. 2010). Most seed-dispersal studies have quantified how variation in dispersal effectiveness influences the early stages of plant regeneration, but we still do not know too much about how dispersal effectiveness translates into plant demography, abundance or dynamics (Howe and Miriti 2004). Here, we explored the allometric effect of ungulate body mass and how this affects the dispersal quality of acacia plants from a demographic perspective. According to our simulations, smaller ungulates (e.g., <35 kg) must remove threefold more seeds than larger ones (e.g., >250 kg) to have comparable effects on acacia population dynamics; this is because large ungulates destroy fewer seeds (2.5-fold; Miller 1995) and enhance the germination of ingested seeds (2.2 times; Rohner and Ward 1999). In general, there is a trade-off between abundance (or density) and body mass of ungulates in all biomes, resulting in proportionally higher abundances of small ungulates in terms of total body mass (Silva et al. 2001). If we consider that seed removal is proportional to abundance or density of seed dispersers (Donatti et al. 2009), the higher seed destruction of small ungulates might be compensated for by their higher abundance; in fact, for the range of body masses in our study system (i.e., from 25 to 800 kg), the relationship given in Silva et al. (2001) predicts that small ungulates are tenfold more abundant than large ones. A third factor of importance is daily food intake, which depends on gut capacity and therefore scales with body mass (Clauss et al. 2007): this would result in a 13-fold increase in food consumption from the smallest to the largest ungulate included in our model. Consequently, the higher abundance and higher food intake per unit body mass of small ungulates could compensate for their higher destruction and lower germination of seeds. Despite the fact that large ungulates negatively affected the acacia population dynamics at medium-to-high browsing intensities, they have higher efficiencies (i.e., they cause less destruction and allow greater seed germination) and can potentially disperse more seeds (due to their proportionally higher daily food intake; Duncan and Poppi 2008); thus, it is probably the positive effects of large ungulates that compensate for the negative effects due to their low abundances. Of course, other qualitative and quantitative components not explored here may have important consequences for the process of acacia regeneration, which include the fate of deposited seeds (i.e., microhabitat differences in seedling emergence and survival, capacity for detection by seed predators) and the spatial use of disperser territory.

Species loss from mutualist guilds, including ungulate dispersers (Bodmer and Ward 2006; Owen-Smith 2007), is an increasingly well-recognized problem (Cordeiro and Howe 2001; Wright et al. 2007; Peres and Palacios 2007), due to its effects on the regeneration processes of many plant species. In general, large-bodied dispersers are usually the most vulnerable due to the fact that they are often the first to be locally driven to extinction, despite their low redundancies and unique ecological services to plant communities (Peres 2000; Peres and Palacios 2007). The main cause of the low recruitment of acacia species is the lack of fruit removal by ungulates (Ward and Rohner 1997; Andersen and Krzywinski 2007), a situation that occurs widely in the Middle East due to their systematic extirpation since the mid-1800s (Evenari et al. 1982). There have been increasing conservation efforts to make this area wild again through the re-introduction of some ungulate species (since the 1980s) and by preventing their extinction (Saltz and Rubenstein 1995; Saltz et al. 2000; Shkedy and Saltz 2000). The regeneration of *A. raddiana* in the Negev desert is of particular concern, because this species is threatened by road-building activities (Ward and Rohner 1997). The preservation of this keystone species (Munzbergova and Ward 2002) is very dependent on fruit removal and dispersal rates (Rohner and Ward 1999) and subsequent germination and recruitment. This suggests that even more ungulate-mediated conservation efforts are necessary to maintain the current acacia populations (Bodmer and Ward 2006). As a consequence, the management of acacia populations strongly depends on the conservation of its seed dispersers, as shown by the present model and in previous empirical studies (Rohner and Ward 1999).

Acknowledgments We are grateful to Christoph Rohner for helping to develop the early idea for the present project, and to Luis Santamaría and two anonymous referees for their useful comments that greatly improved the early version of the manuscript. The work was supported by the Friedrich-Schiller University of Jena (Germany) and by the JEN-A-MACE project (Jena Initiative of Applying Molecular Techniques for the Analysis of Variations of Ecological Processes in Space), funded by the EU (ToK initiative).

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