

# Experimental field test of spatial variation in rodent predation of nuts relative to distance and seed density

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Received: 5 November 2009 / Accepted: 10 February 2010 / Published online: 6 March 2010  
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**Abstract** The spatial context in which seed predation occurs may modify the spatial structure of recruitment generated by seed dispersal. The Janzen–Connell (J-C) model predicts that granivores will exert greater pressure on the parent plant or at those sites where the density of dispersed seeds is higher. We have investigated how the probability of post-dispersal survival of *Juglans australis* varies with nut density across a hierarchy of spatial scales. We experimentally evaluated the survival of 3,120 nuts at three spatial scales: meso-scale ( $\leq 1.5$  ha), as forest sites with two densities of fruiting *J. australis* individuals; intermediate scale ( $< 0.2$  ha), as individual trees with two experimental crop sizes; small scale ( $< 0.1$  m<sup>2</sup>), as microsites with two factors (number of nuts and distance from source). Nut removal coincided with seed predation, a condition that allowed us to test the density-dependent seed predation hypothesis. We found that the probability of nut survival was greater at forest sites with higher *J. australis* density. Nut survival was not affected by nut density in the seed shadow of individual specimens: at sites where *J. australis* density was greater, the proportion of surviving nuts did not

differ between microsites located at different distances from the parent plant, but it was greater at microsites with greater initial nut density. Nut survival depended on the scale at which rodents responded to nut density, being negatively density dependent at the meso-scale and spatially random at intermediate and small scales. At the meso-scale, excess nut supply increased the probability of nut survival, which is in agreement with a model of granivore satiation near the seed source. Rodent satiation at the meso-scale may favour maintenance of sites with high *J. australis* density, where individual trees may have greater probabilities of passing their genes onto the next stage of the dispersal cycle.

**Keywords** Density dependence · *Juglans australis* · Predator satiation · Seed survival · Spatial scale

## Introduction

Rodents can predate almost all of the seeds dispersed from a population during a reproductive season (Wenny 2000; Gulias et al. 2004). Seed predation by rodents occurs mostly after dispersal from the parent plant and is one of the main processes limiting initial recruitment of large-seeded plants (Janzen 1971; Hulme and Benkman 2002; Wang and Smith 2002). This process takes place at the earliest stage of the plant life cycle and produces plant death; therefore, it has a direct effect on plant reproductive success and plays a significant role in determining a population's spatial and genetic structure and dynamics (Janzen 1971; Hulme 1998; Celis-Diez et al. 2004).

The spatial context in which seed predation occurs may modify the spatial structure of recruitment generated by seed dispersal (Janzen 1970; Howe and Smallwood 1982; McCanny 1985). The Janzen–Connell (J-C) model predicts

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Communicated by Jacqui Shykoff.

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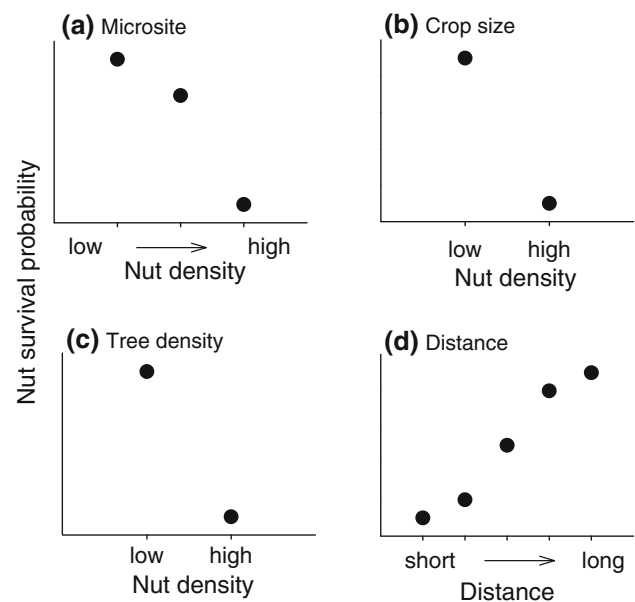
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that granivores will exert greater pressure near the parent plant or at those sites where the density of dispersed seeds is higher (Janzen 1970; Connell 1971); hence, there will be a greater probability of recruitment at a given distance from the parent plant, where the interaction between probabilities of seed arrival and survival to consumption by animals is maximized. Such spatially non-random seed mortality occurs when granivores are strongly attracted to the seed source and is frequently observed among invertebrates (Hammond and Brown 1998), partly because invertebrates are markedly species specific in terms of seed consumption. The generality of the J-C model has been questioned, especially in the case of seed predation by rodents, because several studies have failed to find a consistent relationship between seed survival and seed density or distance to parent plant (Casper 1987; Gryj and Domínguez 1996; Hulme 1997; Alcántara et al. 2000). Other spatial recruitment models, alternatives to the J-C model, consider that seed predation can be density independent or even inversely density dependent when granivores are satiated with a large supply of accumulated seeds (McCanny 1985; Nathan and Casagrandi 2004).

The density of dispersed seeds, which is usually much greater near the parent plant, attracts granivores that become accustomed to these sites as predictable food source areas. This attraction may generate negative distance-dependent seed mortality patterns (Janzen 1970; Nathan and Casagrandi 2004). Hyatt et al. (2003), however, suggested that an increase in seed survival associated with distance to seed source is not a generalized phenomenon, although it may be important in some species. At the population level, the spatial arrangement of plants may have direct effects on the reproductive success of individual plants by influencing foraging decisions of granivores searching for food resources. The density of reproductive plants may also modify patch profitability in terms of food acquisition (Morgan et al. 1997; Marino et al. 2005; Searle et al. 2006); at sites with clumped plants, seed density can be high enough to satiate predators (Janzen 1971; Burkey 1994).

We have conducted experimental research on the effect of seed density and dispersal distance on the post-dispersal survival of nuts of *Juglans australis* Griseb. (Argentine walnut; Juglandaceae). We evaluated the fate of an artificial cohort of 3120 nuts at three spatial scales (forest site, individual tree and microsite) by experimentally manipulating nut density in the seed shadow. In *J. australis*, most seeds accumulate near the parent plant, and a marked reduction in the number of dispersed seeds is expected with increasing distance from the source. Our aims were: (1) to evaluate if (as predicted by the J-C model) the probability of nut survival decreases with an increase in predation rate at sites with higher nut density; (2) to analyse the spatial scaling of



**Fig. 1** Scatterplots showing the predicted probabilities of *Juglans australis* nut survival in relation to nut density at the individual (a, b) and population (c) levels, and in relation to the distance to the parent tree (d)

rodents' responses to nut density and the effects of scaling on nut survival. The probability of seed survival may change across a hierarchy of spatial scales (Hulme and Benkman 2002), and the number of seeds that survive predation may depend on the scale at which predators perceive and respond to the environment. Differences in fruit crop size and spacing among conspecific trees should result in sites with different seed abundances, within a matrix with few or no seeds. At a scale larger than a plant, the patch-matrix relationship (i.e. size and number of forest patches with seeds) depends on the density and distribution of plants that fruited; at a smaller scale, the detectability and availability of seeds may change, depending on the microsite in which they were dispersed.

We predict that at the individual tree level, the probability of nut survival will decrease with an increase in nut density, being lower (1) at microsites receiving a higher number of nuts and (2) at shorter distances from the parent plant, and (3) inversely related to *J. australis* crop size. We also predict that at the population level (4) nut survival should decrease at forest sites with a greater density of reproductive *J. australis* individuals (Fig. 1).

## Materials and methods

### Study area and study species

The study was conducted in Horco Molle (26°47'S, 65°20'W; 700–900 m a.s.l.), a locality situated in Parque

Sierra de San Javier, a protected area of the Universidad Nacional de Tucumán, northwestern Argentina. The area is located in a subtropical montane forest within the southern Yungas ecoregion (Brown et al. 2001; Malizia and Grau 2008), on the lower slopes of the sierras, and includes mature forest with trees of up to 18 m in height and advanced secondary forest sectors. Depending on the slope aspect and the presence of dry ridges or humid ravines, evergreen trees, such as *Blepharocalyx salicifolius* (Kunth) O. Berg (Myrtaceae) and *Cinnamomum porphyrium* (Griseb.) Kosterm. (Lauraceae), or deciduous species, including *Anadenanthera colubrina* (Vell.) Brenan (Fabaceae), *Parapiptadenia excelsa* (Griseb.) Burkart (Fabaceae), *Terminalia triflora* (Griseb.) Lillo (Combretaceae) and *Pisonia zapallo* Griseb. (Nyctaginaceae), are dominant. In Horco Molle, *J. australis* usually grows associated with disturbed sites, such as old clearings, river margins and land slips. Thus, forest sites with a high density of *J. australis* trees (20 trees ha<sup>-1</sup> with a diameter at breast height >10 cm) are frequently intermingled with other sites where *J. australis* individuals grow relatively isolated from other conspecifics (3 trees ha<sup>-1</sup>) (Easdale et al. 2007).

The population of *J. australis* from Horco Molle shows little signs of pre-dispersal seed predation by insects, and no pre-dispersal consumption of drupes or seeds by vertebrates has been observed. The ripening of *J. australis* fruits starts in early January, with a peak of fruit fall between mid-January and mid-February. By the end of February, most nuts have been dispersed. The fruits are drupes that fall to the ground with the fleshy mesocarp still covering the subglobose nuts [mean  $\pm$  standard deviation (SD); length  $26.1 \pm 2.9$  mm, width  $23.7 \pm 2.3$  mm]; predation starts only 2 weeks after dispersal, when the fleshy cover decays. In the northern part of the *J. australis* distribution range, fallen nuts are secondarily dispersed by mammals, including the tapir (*Tapirus terrestris*), which digests the pulp of ingested drupes and passes the nuts intact, and scatter-hoarding seed predators, such as squirrels (*Sciurus ignitus*) and agoutis (*Dasyprocta punctata*). Because the study area is located in the less diverse southern distribution of the Andean montane forest (Ojeda et al. 2008), the array of potential nut predators is narrower than that in the more diverse areas at lower latitudes. Moreover, tapirs were extirpated from the region more than 60 years ago, and collared peccary (*Pecari tajacu*) is restricted to the most undisturbed areas (Nuñez-Montellano et al. 2010) and does not occur within the study site.

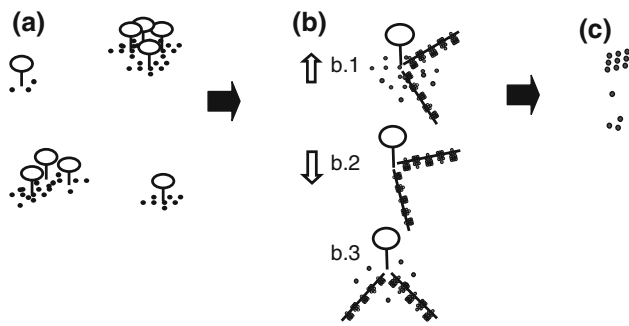
The only vertebrates that may consume nuts at the site are small murids <50 g in body weight. To identify the rodent species that may consume nuts, we placed Sherman live traps near fruiting *J. australis* individuals. The rodents captured were identified and maintained in glass cages that were prepared to supply rodents with nuts and to determine

nut consumption; the rodents were kept in the cage for 3 days or until they consumed the nuts. Individuals of four mice species were evaluated as potential consumers: *Oligoryzomys destructor* (Tschudi) (5 individuals), *Akodon spegazzini* (Thomas) (5), *Akodon simulator* (Thomas) (5) and *Calomys* sp. (5). *Oligoryzomys destructor* (4 of 5 individuals) was the only species capable of gnawing the woody endocarp and consuming seeds. We obtained strong evidence that removed nuts were immediately consumed and that seed removal was not a consequence of nut caching by *O. destructor*. We did not find evidence in the literature of rodents storing nuts for future consumption in the southern Yungas. Furthermore, the mammals of the Sierra de San Javier Park are well known, the park has a rich history of more than 30 years of research in mastozoology and ecology, but there are no published or verbal reports of large seeds cached by rodents (Blendinger and Giannini 2010; Nuñez-Montellano et al. 2010). Moreover, although during this study, we did determine that rodents on many occasions transported marked nuts for short distances (see following section) to more secure places, such as the base of tree trunks, near fallen branches, among exposed roots or in natural cavities, we never found unpredated nuts at these sites.

#### Analysis of nut removal by rodents

We conducted experimental analyses on the removal and survival of nuts at three hierarchical spatial scales (Fig. 2): meso-scale, represented by forest sites ( $\leq 1.5$  ha) with different densities of fruiting *J. australis* individuals; intermediate scale, corresponding to the seed shadow ( $< 0.2$  ha) generated under individual trees situated in those forest sites; microsites ( $< 0.1$  m<sup>2</sup>) that were within the seed shadow of individual trees. At the microsite scale, we considered two factors that may affect nut survival directly: distance from the centre of the parent tree (i.e. the nearest fruiting tree) and number of nuts at the microsite. The microsite allows us to evaluate the effect of nut density at short distances ( $\leq 0.25$  m) independently of other factors, such as plant cover or litter density, which may affect the detectability of nuts or foraging behaviour of rodents.

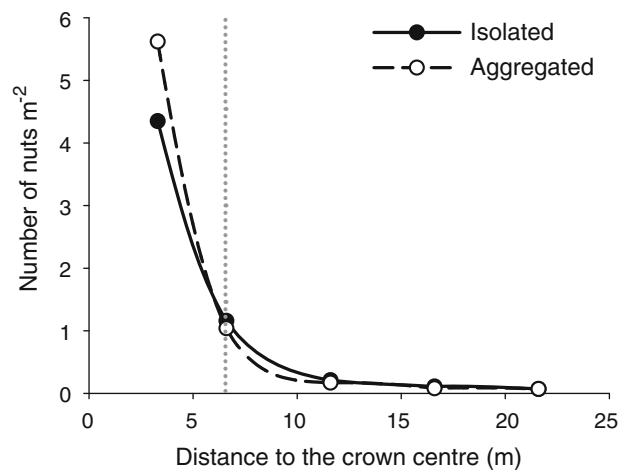
We selected 24 fruiting *J. australis* trees before drupes began to fall. Half of the trees were classified as isolated trees (i.e. at forest sites with trees that were >50 m distant from other fruiting conspecifics), and the other half were classified as aggregated trees (i.e. at forest sites with  $\geq 3$  fruiting trees at a distance of 25–50 m). Only one tree per group was included in the sites with aggregated trees. Within each group of 12 trees (isolated or aggregated ones), we randomly assigned an equal number of trees to three subgroups in which we experimentally modified the supply of dispersed nuts in three different ways: (1) by adding nuts



**Fig. 2** Schematic representation of sampling design, which considers spatial heterogeneity in drupe supply at three spatial scales: **a** “forest sites”, with isolated or aggregated fruiting trees, **b** “trees” of different crown sizes whose drupes fall undispersed to the ground. We measured nut consumption in “microsites” with **c** different nut densities (1, 3 and 9 nuts per microsite) along transects radiating from the trunk of trees with mature fruits

to trees—we increased the density of naturally dispersed nuts by adding 100 mature drupes per week along the radial transects used in the assay to analyse removal by rodents (see below); (2) by collecting nuts around trees—after the initial date of removal assays, we collected all of the naturally dispersed drupes and nuts once a week; (3) control trees—the density of dispersed nuts was not modified. The median crop size of *J. australis* was in the range of 300–500 drupes ( $n = 41$ ); thus, we roughly doubled the number of fallen fruits when we added nuts below trees.

The shadow of fallen nuts was similar at all trees, with maximum values under the canopy and a strong decrease in density with increasing distance from the source (Fig. 3). Under each of the 24 trees, we established two radial transects and recorded the removal of marked nuts weekly in a field design of 13 nuts (in experimental depots with an initial number of 1, 3 and 9 nuts per microsite, respectively) at each of the five distances from the trunk. We set the two transects departing from the projection of the crown centre and extending to the periphery; whenever possible, the two transects were set perpendicularly, but still avoiding steep slopes or overlap with the seed shadow of other *J. australis* individuals. Five distances were defined from the centre along the transects. The first distance corresponded to half of the crown radius; the second, to the vertical projection of the crown perimeter; the remaining three distances were 5 m apart. At each distance, we systematically marked three microsites where we placed the nuts: one on the transect line and the other two 1 m away from each side of the transect and perpendicular to it; at each microsite, we randomly placed one of the three numbers of nuts (1, 3 or 9) without the fleshy mesocarp. Each nut was marked with permanent ink and tied to a stake with a thread that was solidly glued to the nut. The threads prevented nut movement by surface water drainage after intense rainfall but allowed easy removal of nuts by rodents. Permanent ink allowed us to



**Fig. 3** Nut dispersal from aggregated and isolated fruiting trees, based on mean density of nuts dispersed at five distances from the crown centre. Vertical dotted line Average radius of the crown

identify remains of consumed nuts moved away from the experimental depots; such movements were typically not more than a few metres. We placed the marked nuts on the ground between January 17 and 19, 2007, about 2 weeks after the start of mature drupe falling and when most of the *J. australis* individuals in Horco Molle had mature fruits at the dispersal stage. Artificially placed nuts on the ground closely mimicked the natural deposition of nuts in the study site, with nuts exposed on the ground after quick pulp decomposition without secondary dispersal by animals. We made four visits at 1-week intervals and recorded the number of marked nuts surviving at each microsite.

Because the initial removal of nuts was very high, we made an additional assay by comparing nut removal in forest sites of low and high *J. australis* density. On 9 February 2007, we started evaluating daily survival of 50 nuts for 2 weeks. At each site, we placed one nut (marked and fixed to a stake) at 5-m intervals along the transect, resulting in a total of 25 nuts per transect.

#### Statistical analyses

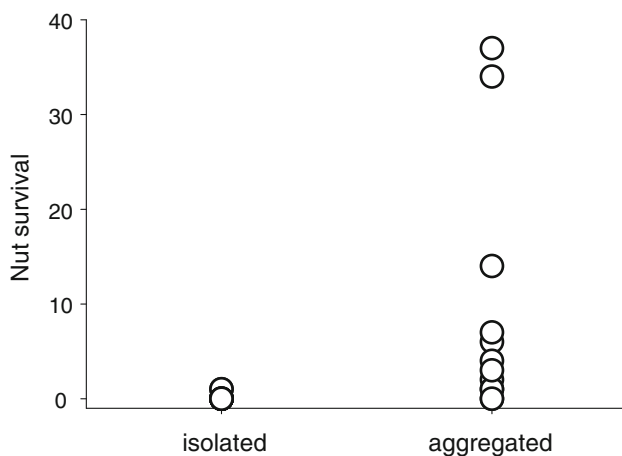
We used the “survival analysis” module of Statistica ver. 6.0 (2001) (StatSoft, San Diego, CA) to compare the survival times of nuts between forest sites (i.e. at the meso-scale). We used log-rank tests, a non-parametric test recommended for evaluating the effect of categorical predictive variables. To investigate the effect of nut density on weekly nut survival at different spatial scales (forest site, tree and microsite), we used the non-parametric Kruskal–Wallis test, comparing the number of unpredated nuts per time interval. We determined the statistical significance of differences in survival between all pairs of cases with post hoc multiple comparisons test. We could not analyse the different effects

together because the strongly biased distribution of survival data did not fit distributions of the exponential family.

**Results**

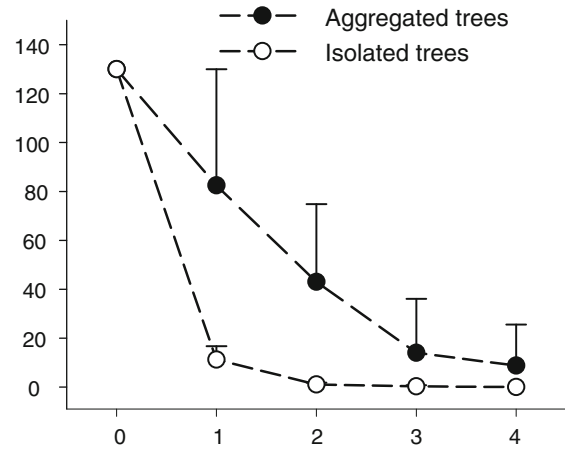
Removal of nuts from the experimental depots by small rodents, such as *Oligoryzomys destructor*, was extremely high (>96%) during the four sampling weeks. During the 4 weeks in which nut removal was experimentally evaluated, the time of nut survival differed significantly between forests sites (log-rank test  $L = -27.46$ ,  $P < 0.0001$ ). Nut removal during the first week was much greater at sites with isolated *J. australis* individuals (average removal 86–92%, depending on the treatment) than at sites with greater *J. australis* density (34–37%; Fig. 4). At the end of the experiment, the number of nuts surviving consumption by rodents was greater at forest sites with densely aggregated *J. australis* individuals [mean proportion  $\pm$  standard error (SE),  $0.065 \pm 0.011$ ] than at sites with isolated *J. australis* individuals within the forest matrix ( $0.001 \pm 0.001$ ) (Mann–Whitney  $U$  test  $z = 3.47$ ,  $n_1 = 354$ ,  $n_2 = 360$ ,  $P = 0.0005$ ; Fig. 4). Within each forest site, nut survival time was not affected by nut density, measured with the experimental addition or subtraction of drupes under individual trees (Fig. 5). In both situations, a similar removal pattern between the two experimental treatments and control was observed.

Daily survival of 50 nuts evenly distributed on the two transects differed significantly between forest sites with different *J. australis* density 14 days after the start of the experiment (log-rank test  $L = -4.36$ ,  $P < 0.0001$ ). During

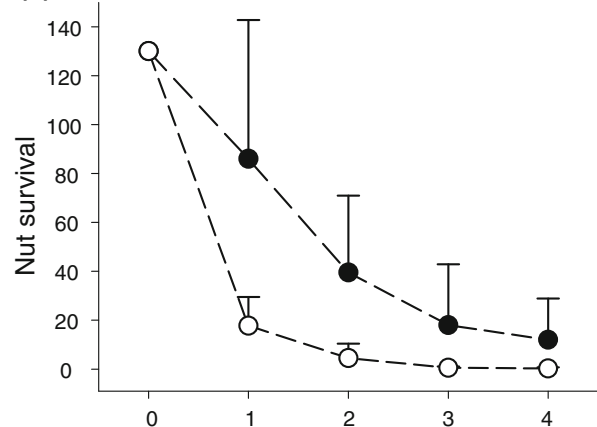


**Fig. 4** Number of nuts surviving after 4 weeks under trees located in forest sites where *J. australis* density was low (isolated trees,  $n = 12$ ) and high (aggregated trees,  $n = 12$ ). The initial number of nuts was 130 per tree for all trees

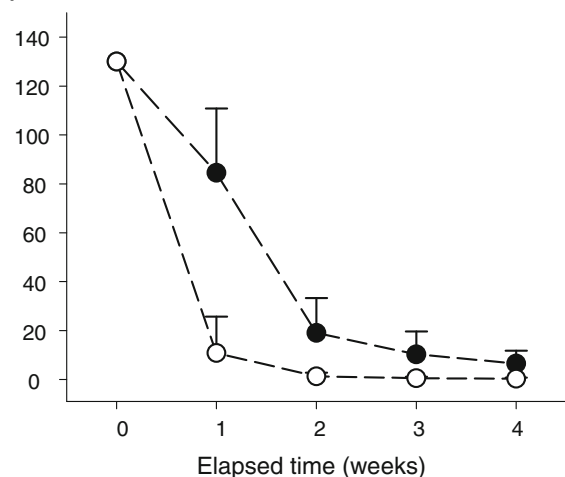
**(a) Addition of drupes**



**(b) Removal of drupes**

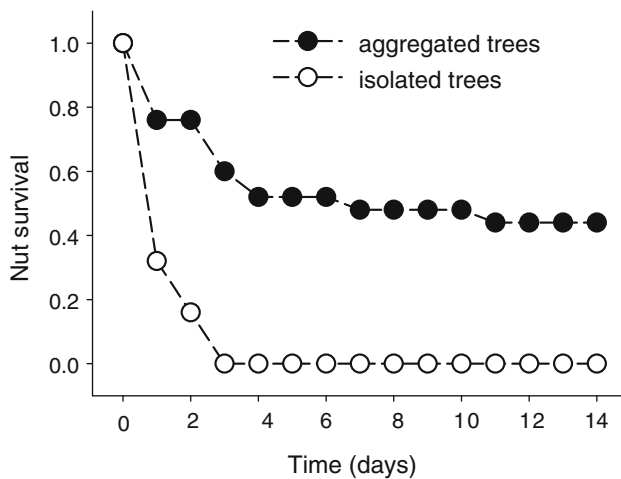


**(c) Control**



**Fig. 5** Number of surviving nuts (mean  $\pm$  standard deviation) in field experiments with the addition or removal of drupes under individual trees. In each treatment ( $n = 4$  trees), the initial number was 130 marked nuts per tree. In the drupe addition treatment (a), 100 drupes were added weekly, evenly dispersed in a radius = 25 m from the projection of the crown centre. In the removal treatment (b), all drupes dispersed in a similar radius were collected weekly





**Fig. 6** Survival of nuts in two forest sites with different densities of fruiting *J. australis* individuals. In each site, 25 nuts were arranged, systematically spaced (0.5-m intervals) along a line transect

the first days, the removal rate was much higher at the site with a low density of fruiting *J. australis* individuals (Fig. 6); indeed, all nuts were removed after 3 days. At the site of greatest *J. australis* density, the probability of nut survival increased after the first week of exposure.

To explore the effect of removal at finer spatial scales (i.e. tree and microsite), we analysed nut survival only within forest sites with high *J. australis* density because, given the high predation rate (99.9%) in sites with low tree density, a more detailed analysis was unnecessary. The proportion of the initial number of surviving nuts did not differ between trees with different densities of dispersed nuts or between microsites located at different distances from the parent plant (Table 1). From the third week onwards, the proportion of surviving nuts was significantly greater at microsites with a higher initial density of nuts (groups of nine nuts) than at microsites with one or three initial nuts (post hoc multiple comparisons test; Table 1).

## Discussion

Variability in the supply and predation of nuts of *J. australis* did not covary among scales; hence, nut survival depended on the scale at which rodents responded to nut density. At the spatial scale that included forest sites (i.e. the meso-scale), we found a non-random pattern that depended on nut density, which is opposite to the pattern predicted by the J-C model (Janzen 1970; Connell 1971), whereas nut survival was density independent at finer spatial scales. Our results indicate that at the meso-scale, an excess of nut supply increases the probability of nut survival. This negative density-dependent survival fits a model of granivore satiation near the seed source (Janzen 1971;

**Table 1** Mean nut survival at weekly intervals at two spatial scales (i.e. seed shadow of an individual tree and microsite) in forest sites with a high density of fruiting *Juglans australis* individuals

Scale	1 week	2 weeks	3 weeks	4 weeks
<b>Tree</b>				
$H_{2;12}$	0.81	1.43	0.78	2.10
$P$	0.67	0.49	0.68	0.35
<b>Microsite</b>				
Distance				
$H_{4;45}$	2.57	4.79	0.63	0.41
$P$	0.63	0.31	0.96	0.98
Number of nuts				
$H_{2;180}$	0.10	4.81	11.88	12.57
$P$	0.95	0.09	0.003*	0.002*

At the tree scale, we compared experimentally two densities of dispersed drupes (trees with the addition or extraction of drupes and control treatment). For the microsite, we compared the effect of distance from the centre of the crown of the parent plant (5 distances: under the crown, periphery of the crown projection, at 5, 10 and 15 m from the periphery of the crown) and the number of nuts per microsite (1, 3 and 9 nut per microsite)

\* Survival significantly greater in groups of nine nuts (post-hoc multiple comparisons test among groups)

Nathan and Casagrandi 2004) and acted at a greater spatial scale than that at which rodents could track nut supply.

In contrast to most studies on the consumption of large-seeded species by rodents, our study was characterized by the absence of scatter-hoarding mammals that disperse nuts by burying them under the topsoil, a condition that allowed us to test the J-C hypothesis. That is, we could attribute the high level of nut disappearance to seed predation per se, highlighting its importance as the main mechanism affecting seed fate. In temperate deciduous forests in the Northern Hemisphere, several species of *Juglans* are consumed by scatter-hoarding species of squirrels and mice (Vander Wall 2001; Tamura and Hayashi 2008; Zhang and Zhang 2008). In tropical and subtropical forests in the Neotropics, agoutis are the main seed dispersal vectors for some large-seeded plants (Jansen et al. 2004). Although squirrels (*Sciurus ignitus*) and agoutis (*Dasyprocta punctata*) consume and store nuts of *J. australis* (P. G. Blendinger, personal observation), they are absent in the southernmost portion of the *J. australis* distribution range. It is known that some small-sized Neotropical mice cache seeds (Giannoni et al. 2001; Campos et al. 2007), but it appears that scatter-hoarding of large-seeded species by mice is an uncommon phenomenon in the Neotropics (but see Brewer and Rejmanek 1999). Thus, it is possible that in the southern Yungas forests, nuts are only effectively dispersed by large mammals, such as tapirs; however, tapirs were extirpated from this region by humans in the last century (Nuñez-Montellano et al. 2010).

According to the J-C model, seed survival at the population level is expected to correlate negatively with the density of conspecifics fruiting simultaneously because the fraction of habitat exposed to specific predators increases with the density of seed-producing trees (Schupp 1992). In our study, however, weekly nut survival was much lower at forest sites with low *J. australis* density, where 98.3% of nuts were removed during the first 2 weeks. Our evaluation of the daily survival of nuts at forest sites with high and low *J. australis* density yielded similar results, since 100% of nuts were consumed in only 3 days at the site of low *J. australis* density. In general, the data reported in the literature are also not consistent with model predictions at spatial scales encompassing populations. In tropical forests, studies on two trees of the understorey of Central America, *Gustavia superba* (Lecythidaceae) and *Faramea occidentalis* (Rubiaceae) (Forget 1992; Schupp 1992), and on several species of mangroves of the genera *Avicennia* (Verbenaceae), *Bruguiera* and *Rhizophora* (Rhizophoraceae) (Smith et al. 1989), reported that the proportion or number of surviving seeds was greater at sites with a greater density of adult reproductive trees. Chauvet et al. (2004) found that of the two canopy species of Sapotaceae, only in one (*Manilkara huberi*) was seed survival greater at sites with a low density of conspecifics, whereas the other species (*Chrysophyllum lucidifolium*) had an opposite pattern. Information on subtropical forests is less abundant but shows a similar trend; for example, in a subtropical forest of China, removal of seeds of *Castanopsis fargesii* (Fagaceae) by rodents decreased with increasing seed density in the population (Xiao et al. 2005).

The analysis including spatial scales smaller than the meso-scale lends weak support to the hypothesis of spatially non-random predation of *J. australis* nuts. In the seed shadow generated at a single tree, nut survival did not vary with distance from the parent plant or with crop size. In other plant-granivore systems in which rodents were the main seed predators, a spatially random mortality at the seed shadow scale was also observed (e.g., Casper 1987; Hulme 1997; Alcántara et al. 2000). In other systems, higher seed mortality was detected at greater distances where seed density was lower (Takeuchi and Nakashizuka 2007), whereas an increase in seed survival at a greater distance from the parent plant is a rare phenomenon (Hyatt et al. 2003), which contradicts predictions of the J-C model.

At the microsite scale, survival of *J. australis* nuts did not vary with distance from the parent plant or with nut density, except for those nuts that were at microsites where the initial nut density was greater and which were located at forest sites with high *J. australis* density; at these latter sites, mean survival increased at the third week of expo-

sure. Because *Oligoryzomys destructor* consumes one or two nuts at a time (P.G. Blendinger, personal observation), the positive effect of nut density may be better reflected in encounter patterns of experimental nut depots than in consumption patterns (Hulme and Borelli 1999). Assuming that nut depots had equal chances of being found, then the probability of survival of individual nuts at microsites with a greater number of nuts was higher than at sites with a smaller number of nuts because only some nuts were consumed at each foraging event.

Our results suggest that the density of dispersed nuts, a scale-dependent measure, would have been perceived by rodents as a randomly distributed resource within forest sites. The post-dispersal predation of nuts was due almost entirely to *O. destructor*, which was very efficient in detecting microsites with nut depots in forest sites (100 and 97.5% of experimental nut depots were found in forest sites with low and high *J. australis* density, respectively) but had no ability to track variation in nut supply among forest sites. In forest sites with a high density of fruiting *J. australis* individuals, nut supply would have been high enough to induce satiation in rodents, allowing the survival of a higher proportion of nuts than in sites with a low seed supply. Temporal satiation of granivorous vertebrates has been mostly explored at the population level in events of synchronous, episodic seed production (“mast-seeding events”) (e.g. Curran and Leighton 2000; Xiao et al. 2005; Lázaro et al. 2006), although satiation in predators may also occur in forest patches or habitat types with high seed density (Janzen 1971; Forget 1992; Schupp 1992; Alcántara et al. 2000).

Although the negative density dependence found in forest sites could be explained by the spatial inconsistency between population variability of nut supply and abundance of rodents, the latter did not track nut supply at this scale, suggesting that satiation in rodents was induced by an overabundance of food. Satiation of rodents may act as a mechanism regulating the survival of nuts of *J. australis* at the meso-scale. Between-forest site variability in post-dispersal predation generates sites with either a high or low probability of seed survival and can modify the initial recruitment template generated by dispersal (Forget 1992; Hulme 1997; Calviño-Cancela 2007). However, modification of the spatial patterns of relative nut abundance between habitats may not have a qualitative effect on the population in two situations: when the amount of predated seeds is proportional to their density in different site types (Herrera et al. 1994; Alcántara et al. 2000) or if it is greater at those sites where recruitment is not limited by seed availability (Calviño-Cancela 2007).

We did not follow the fate of nuts that survived until the completion of the field study. However, if the greater proportion and number of surviving nuts at forest sites with

high *J. australis* density determines a spatial pattern that is maintained in successive stages of the dispersal cycle (Wang and Smith 2002), this greater nut survival could act as a mechanism that would favour the maintenance of sites with high *J. australis* density and individual trees whose probability of passing genes onto the following stage of the dispersal cycle would be increased. Nut production at the study site was similar in the year following our study; however, seed survival differed strongly, and many nuts could be found below parent trees 9 months later when seeds started to germinate. Reduced nut consumption could reflect lower population densities of *O. destructor* or higher availability of alternative food resources. Beyond the ecological mechanisms promoting between-year differences, the possibility remains that in years of lower nut-predation pressure, seed survival may be affected by processes acting at finer spatial scales than forest sites and may be responsible for the recruitment of new individuals.

## Conclusions

Despite the limitations to our study, our findings provide an empirical test for theories of seed survival with respect to density-dependent predation and the spatial scaling of rodents' responses to seed density. The consequences of nut predation on the fate of the offspring may strongly depend on the spatial scale at which predation occurs. The processes associated with nut survival acting at the population scale possibly do not operate at the scale of the microsite where a nut was deposited or near an individual tree, and vice versa (Schupp 1992; Rey et al. 2002). Kollmann (2000) found that the principal spatial differences in seed predation by rodents are more likely to occur at a habitat scale (10–10,000 m<sup>2</sup>) than at the microhabitat scale (0.01–10 m<sup>2</sup>) because the results obtained at the latter scale are usually unclear. If the spatial context of seed predation affects recruitment in the population, it may favour dispersal strategies that tend to minimize predation. Offspring mortality in species with short seed-dispersal distances, such as *J. australis*, would be greater than that in species whose seeds are dispersed over longer distances (Jansen et al. 2008); thus, the former may benefit from a strategy of increased seed supply at the individual or population level to induce satiation in predators.

**Acknowledgments** Permission for conducting research work in Horco Molle (2006–2007) was granted by Parque Sierra de San Javier of the Universidad Nacional de Tucumán. Lucía Zarba, Juliana Rajmil, Marisol Mata and Gustavo Sánchez helped us with field data collection. We thank Johannes Kollmann and Jacqui Shykoff for helpful comments on the manuscript. The experiments carried out in this study comply with the current laws of Argentina.

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