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Journal of Arid Environments 73 (2009) 773–783

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Patterns of frugivory, seed dispersal and predation of blue fan palms (*Brahea armata*) in oases of northern Baja California

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ARTICLE INFO

Article history:
Received 15 July 2008
Received in revised form
15 February 2009
Accepted 27 March 2009
Available online 21 May 2009

Keywords:
Baja California
Beetles
Blue fan palm
Brahea armata
Desert oasis
Frugivory
Palm–animal interactions
Rodents
Seed dispersal
Seed predation
Spatial association pattern

ABSTRACT

Variations in spatial and temporal availability of fruits and seeds in oases are important not only for animal seeking resources, but also for palm population dynamics. We explored spatial association patterns between avian frugivores and blue fan palms in two natural palm patches of Baja California. Spatial patterns were analyzed at the individual tree and at 2 ha patches. We evaluated seed predation by vertebrates and invertebrates, and vertebrate seed dispersal around palms. Birds responded to fruit aggregation at the individual tree and the patch scales, but responses varied between patches. Palm fruit variables—the quantity and the phenological phase—and avian visits showed strong spatial aggregation and association at both scales in one patch, but not in the other. The intensities of seed predation and seed dispersal were significantly higher directly below palms than at >3 m away from them. Patches differed in the intensity of seed predation around palms and in the diversity of mammalian dispersers, but not in the intensity of seed dispersal. Blue fan palms function as important resources' focuses for a great number of animals that use palm oases as corridors, bringing seeds as they move and connecting isolated populations of palms.

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1. Introduction

Desert ecosystems throughout the world are characterized by a high degree of patchiness, with sparse vegetation cover often arranged as two-phase mosaics of vegetated and bare ground patches (Ezcurra et al., 1988; Felger et al., 1992; Maestre and Cortina, 2002). They are also characterized by having relatively rare safe germination sites interspersed among more abundant, unfavorable sites (Henderson et al., 1988). The species composition of these patches results largely from past large-scale environmental changes, species migration (Turner, 2004), and movement and accumulation of seeds in pits due to both animal activity and wind, which traps them in naturally occurring depressions (DeSoyza et al., 1997; Reichman, 1984; Whitford, 2002; Whitford and Kay, 1999). Physical crusts, surface soil, roots and rock fragments are also relevant in water, seed and nutrient fluxes influencing the dynamics of patches (Maestre and Cortina, 2002; Poesen and Lavee, 1994; Seghieri et al., 1997; West, 1990). However, patchiness in deserts is not limited to spatial patterns of plants in relation to soil and topography; it is also a function of plant–plant (Miriti, 1999; Miriti et al., 2001) and plant–animal interactions (García and Chacoff, 2007; García et al., 2005), as well as the effects of animals on soil properties through fecal deposition and the redistribution of seeds (Whitford, 2002). Large trees serve as refuge sites for birds and mammals that utilize shade or consume fruit, functioning as important focal species for the development and maintenance of patches (Dean et al., 1999; Milton et al., 1998). Although seed dispersal in deserts may be mainly governed by episodic wind events and water flow through landforms and topography, the spread of some of these patches is due in part to seed dispersal by animals (Whitford, 2002).

In northern desert regions of Baja California, remnant vegetation patches from an ancient paratropical forest (Peñalba and van

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0140-1963/$ – see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jaridenv.2009.03.007

Devender, 1998; Willis and McElwain, 2002) are found today as isolated refuges on mountaintops and along canyons that still conserve wet conditions (Ezcurra et al., 2006; Franco-Vizcaíno et al., 2007; Henderson, 1964, 1971). Dominated by fan palms in the *Washingtonia* and *Brahea* genera, these remote oases provide particular microclimatic conditions that support contrasting biotic communities and offer fundamental ecological services. They regulate water regimes and control erosion by serving as sedimentation areas and filtering basins, also acting as sources of biodiversity and stopover sites for migrating birds (Cornett, 1985, 1989; Cornett et al., 1986; Grismer and McGuire, 1993). Life in deserts is thus inextricably linked to oases; loss of these ecosystems can cause serious damage to the local economy and human welfare. Although they are important as water and biodiversity reservoirs and they have serious implications for conservation priorities in the region, desert oases constitute one of the less studied ecosystems in northern Baja California.

Palms offer fruits with highly nutritious mesocarps and endosperms that constitute a critical reward for animal dispersers (Zona and Henderson, 1989). However, in at least some cases, dispersal is considered a risky business for palm seeds, since they are much more likely to be eaten than dispersed (Henderson, 2002). Commonly dominated by plants that live for decades and even centuries (Turner et al., 1995, 2003; Vasek, 1980), the underlying mechanisms of desert vegetation dynamics are difficult to study (Whitford, 2002). Woodrat (*Neotoma*) middens that contain remains of plants, invertebrates, and vertebrates constitute a significant tool for tracking climate/vegetation changes and for the reconstruction of the past environments and climates (Betancourt et al., 1990; Wells, 1976). A particular study from a granite boulder area near Cataviña, Baja California documented relative plant abundance and distribution different from today's (Sankey et al., 2001). The abundance in the midden of mesquite and other taxa, which today live over 100 m from the midden, suggests greater soil development on boulder surfaces and a relatively more mesic climate, which allowed these plants to expand into more marginal habitats (Sankey et al., 2001). In addition, because ice age megafauna were likely quite different from today's seed dispersers and predators (Felger, personal communication), the large fruits and hard seeds of *Braheas* may have co-evolved with those extinct animals.

Blue fan palms (*Brahea armata*), which are endemic to Baja California, seem to be particularly efficiently adapted to harsh environmental conditions. As the climate became drier and warmer from 5–1.8 million years ago (beginning in the late Miocene time), they became restricted to these riparian and remote habitats (Axelrod, 1979; Millar, 1996; Thorne, 1986). This fan palm is classified into the Coryphoideae, one of the five monophyletic subfamilies of the Arecaceae (Dransfield et al., 2005), with age estimations that suggest a potential longevity exceeding 500 years (Bullock and Heath, 2006). While most palm species are currently widespread in tropical and subtropical regions of the world (Bjorholm et al., 2005, 2006; Corner, 1966), some coryphoid species live at the limit of the family's distribution (Felger and Joyal, 1999; Kvacek and Herman, 2004; Mai, 1995; Palamarev et al., 2000; Uhl and Dransfield, 1987) constituting patches of life surrounded by mountains and desert plains at these latitudes (Ezcurra et al., 2006; Felger et al., 2001; Henderson, 1971; Turner et al., 1995).

Since heterogeneity is significant in arid regions (Valentin et al., 1999; Whitford, 2002), a hierarchical patch structure approach may be critical to progress in understanding how organisms respond to resource patchiness in space and time, as well as the ecological and evolutionary consequences of these interactions (Dungan et al., 2002; Kotliar and Wiens, 1990). Frugivores and seed predators must cope with fruit and seed-resource heterogeneity and may use particular mechanisms that allow effective resource tracking (Fleming, 1992; García and Ortiz-Pulido, 2004). In turn, the ecological and evolutionary outcomes of seed dispersal by animals depend on the spatial and temporal scales at which frugivory patterns emerge (García and Ortiz-Pulido, 2004; Herrera, 1998; Jordano, 1995; Kollman, 2000; Thompson, 2002). For example frugivores acting at small spatial scales, selecting among different fruits within the same individual plant, might affect sib-competition and paternity patterns within the extent of plant populations (Bertin, 1988). At larger scales, selective dispersal among patches may affect plant population dynamics (Herrera et al., 1994; Jordano and Godoy, 2002). At an even higher scale, the variation in the fruit–frugivore patterns among geographical regions might promote geographical mosaics of coevolution (Jordano, 1993; Thompson, 1994, 2002). From an evolutionary point of view, the scale at which interactions occur can influence the selective pressures of animals on plants. In this sense, particular plant–frugivore interactions might dilute or relax selective pressures by frugivores on plants in the long term (Herrera, 1998; Levey and Benkman, 1999; Wehncke and Domínguez, 2007). Blue fan palm desert oases of northern Baja California offer an interesting natural scenario to evaluate patterns and scales of predation/dispersal processes affecting fruits and seeds, since fruits occur as a strongly heterogeneous resource which varies among successive spatial and temporal extents. Understanding these mechanisms will help in elucidating how animals respond to water pulses, and which factors control palms at the margin of the family distribution (S. Bjorholm, personal communication; Dransfield et al., 1990).

It is known that frugivory, seed dispersal and seed predation may affect the resultant recruitment patterns and the ecological dynamics of plant populations (Herrera, 1998; Jordano, 1995; Thompson, 2002). Moreover, post-dispersal seed predation by vertebrates and invertebrates is often considered the principal process underlying plant recruitment patterns, as well as the major cause of plant mortality (Hulme, 1993; Janzen, 1971; Packer and Clay, 2003; Schupp, 1990;). In northern desert areas of Baja California, where many organisms live at or very near the threshold for surviving climatic extremes, the availability of desert oases with palm fruits arranged in patches and interspersed along canyons is critical for animal subsistence (Whitford, 2002). Since palm trees are the dominant vegetation, and the focus for birds and mammals as shelter and resource concentration sites, acting as keystone species in their habitat (Felger, 1999), we evaluated seed dispersal by vertebrates and seed predation activities by vertebrates and invertebrates around blue fan palm trees in these oases. Bullock (1980) suggested that omnivore vertebrates may consistently transport seeds to wide distances and generate quite heterogeneous seed shadows in this kind of environment. Here, we evaluated the strength of the interaction between palm fruits and the frugivore bird community by studying the spatial pattern and associations between two palm fruit variables—the quantity and the phenological phase of fruits—and avian visits. We explored the consistency of patterns at two different scales, 'patch' (2 ha) and 'within-patch' (0.2 ha), in blue fan palm canyons of the Cataviña area of Baja California.

Given that the seed dispersal syndrome of *Brahea* fruits seems to correspond to endo-zoochory, probably performed by the now-extinct Pleistocene megafauna (Felger, personal communication), the interactions of blue fan palms with present-day fauna are important elements in understanding current ecological processes and dynamics occurring in desert oasis ecosystems. Finally, since palm oases are distributed as distinct patches in space and time, frugivory, seed dispersal and post-dispersal seed predation processes within and between oases are of great demographic importance.

2. Methodology

2.1. Study areas

We selected the Cataviña oasis (N29°45′, W114°40′) as study area to evaluate frugivory, seed dispersal and seed predation activities in detail. Cataviña is part of the federal Valle de los Cirios Natural Protected Area and is located within Forrest Shreve's Vizcaíno Region, also known as the Central Desert of Baja California (Shreve and Wiggins, 1964). The geological history of this area is visible in the ancient granite core. Erosion has carried away soils that were deposited in this region 100 million years ago (Durham and Allison, 1960; Sankey et al., 2001). The area's climate is very dry, warm to temperate, with precipitation in the cool winter season—61–91% of the total falls in November through April (Bullock, 2003). The canyon has a concave topography composed of granite rocks with a large flat surface covered with fine granitic sand. In addition to *B. armata*, we also registered three non-reproductive *Washingtonia filifera* palms in Santa Inez, one of the study patches. We selected two study plots in naturally formed patches of approximately 2 ha along the San Antonio canyon: Santa Inez (617 m a.s.l.) and San Antonio (609 m a.s.l) plots, hereafter SI and SA, respectively (Fig. 1). The plots were separated by a straight-line distance of 1.5 km and have an elongated configuration of approximately 400 × 35 m; the size of the whole study area was approximately 1.2 km^2. San Antonio was the farthest plot from the local settlement of Cataviña and the highway, but it was the most commonly used path by off-road tourism and cattle. This is a very wide canyon with scattered adult palm trees. In contrast, the Santa Inez site was less frequently visited by tourists and occasionally used by cattle for resting under palm trees. This canyon is narrower than the other and adult palm trees are more aggregated. We visited the area in different seasons and selected September 2006 for studying palm fruit–bird interactions, since fruits were seen to be more palatable to animals during this period. Seed predation activity around focal trees was studied during two months of the same fruiting season, September and November 2006, because sufficient numbers of seeds were found on the ground during these months. Seed dispersal activity was studied in two contrasting seasons, September 2006 and February 2007.

2.2. Interactions between palms and the frugivore bird community

In order to explore the strength of the palm fruit–avian frugivore interaction and its dependence upon the spatial heterogeneity of resources in this desert ecosystem, we evaluated the spatial associations between two palm fruit variables (quantity and phenological phase) and avian visits, using the Spatial Analysis by Distance Indices (SADIE) method, which was developed explicitly for the spatial analysis of ecological data in the form of counts (Perry, 1998; Perry and Dixon, 2002; Perry et al., 1999). We then explored the consistency of spatial patterns at two different scales, 'patches' of 2 ha and 'within-patches' of 0.2 ha. Patches represented the approximate size of naturally distributed groups of blue fan palms commonly found along these canyons. The smallest 'within-patch' scale represented the 'tree level' or a restricted data set including only those cells having on average one palm tree. Our sampling extensions are intended to be wide enough to include the maximum spatial variability of the ecological phenomena studied (Dungan et al., 2002). By removing the contrast among areas with and without trees, this method effectively reduces the scale studied to that of the individual palm tree. The within-patch pattern with only grid cells including adult plants may have different clustering indices compared to the between-patch pattern, and may yield important information on local spatial interactions (Perry and Dixon, 2002).

In order to convert palm tree location information to count data, plots were divided into grids of contiguous cells of 5 × 5 m^2, and the quantity and phenological state of fruits and avian visits were estimated for each sampling unit. The grain, or the size of the cell area, was chosen following guidelines according to Dungan et al. (2002), based on previous observations of the seed dispersal and predation processes, and the recruitment patterns of blue fan palms. Additionally, it was also selected as it includes on average one individual tree per cell (Perry and Dixon, 2002). Cell size was maintained constant at 5 m × 5 m through all analyses at both scales.

All reproductive adult palms were measured in height, tagged for further phenological studies, and mapped, with their locations geo-referenced in each plot. Fruit availability per plant was estimated as the abundance of fleshy fruits on a five-point scale for each palm tree (0 = no fruits, 1 = 25% of the plant with fruits, 2 = 50% of the plant with fruits, 3 = 75% of the plant with fruits, and 4 = 100% of the plant with fruits). Each category represents an estimation of the percentage of fruits that a palm tree was bearing at the time of observation from its potential total capacity. The number of fruits is highly variable in palm species (Henderson, 2002), from one or two to 27,000 fruits per infructescence in *W. filifera* (Cornett, 1989). Blue fan palm fruits were counted in six infructescences of different trees in Cataviña and the mean number was estimated as 900 ± 438.2 fruits per infructescence. The relative size and number of fruits per infructescence in blue fan palms vs. *W. filifera* seem to be in accordance with the general trend in palm species—the larger the fruit, the smaller the number per infructescence (Henderson, 2002). Fruits of blue fan palms measured from 2 to 2.5 cm in diameter, while those of *W. filifera* were approximately 1 cm. Blue fan palm trees in Cataviña produced from 1 to 6 infructescences, so therefore a palm was in category 4 when 100% of the plant was with fruits or when the maximum number of infructescences full of fruits was present. We also estimated the phenological state of fruits per palm tree as the change in colors that occurs in fruits according to their maturation phases on a five-point scale (0 = no fruits, 1 = green, 2 = green to yellow, 3 = orange, 4 = brownish, 5 = dark brown) (Plate 2, Suppl. data). Phenological phases going from one to three corresponded to immature, four to mature, and five to old dry fruits. To obtain information about the number of bird visits to individual fruiting palms, we performed consecutive observation bouts of 10 min during 1–2 h—early mornings and late afternoons—for each plot. We registered avian visits to marked palm trees recording the identification number of the palm and the number of visits per bird species. After each 10-min bout the position of observer changed following a circuit around the plot, taking care not to disturb bird activity.

2.2.1. Spatial patterns of avian visits and availability of fruits

Spatial patterns of the quantity and phenological state of fruit and bird visitations were analyzed using SADIEShell software (version 1.22; Kelvin F. Conrad and IACR Rothamsted, 2001; Perry, 1998; Perry et al., 1999). The analysis involves the detection and testing of non-randomness in data, its measurement by indices, and an assessment of the degree to which the count in each unit contributes to the overall pattern. Spatial patterns by SADIE were obtained on the basis of permutation of count data, randomly reassigning each of the total individuals in the sample to a new sample unit. With the counts of individual events in a grid of contiguous sample units, we could calculate the total distance (D) necessary to achieve the same number of points in each sample unit (distance to regularity). We obtained a formal test of randomness and an index of aggregation (I_a) resulting from the division of the observed value of D by the mean from the randomization procedure. Usually an aggregated variable has an

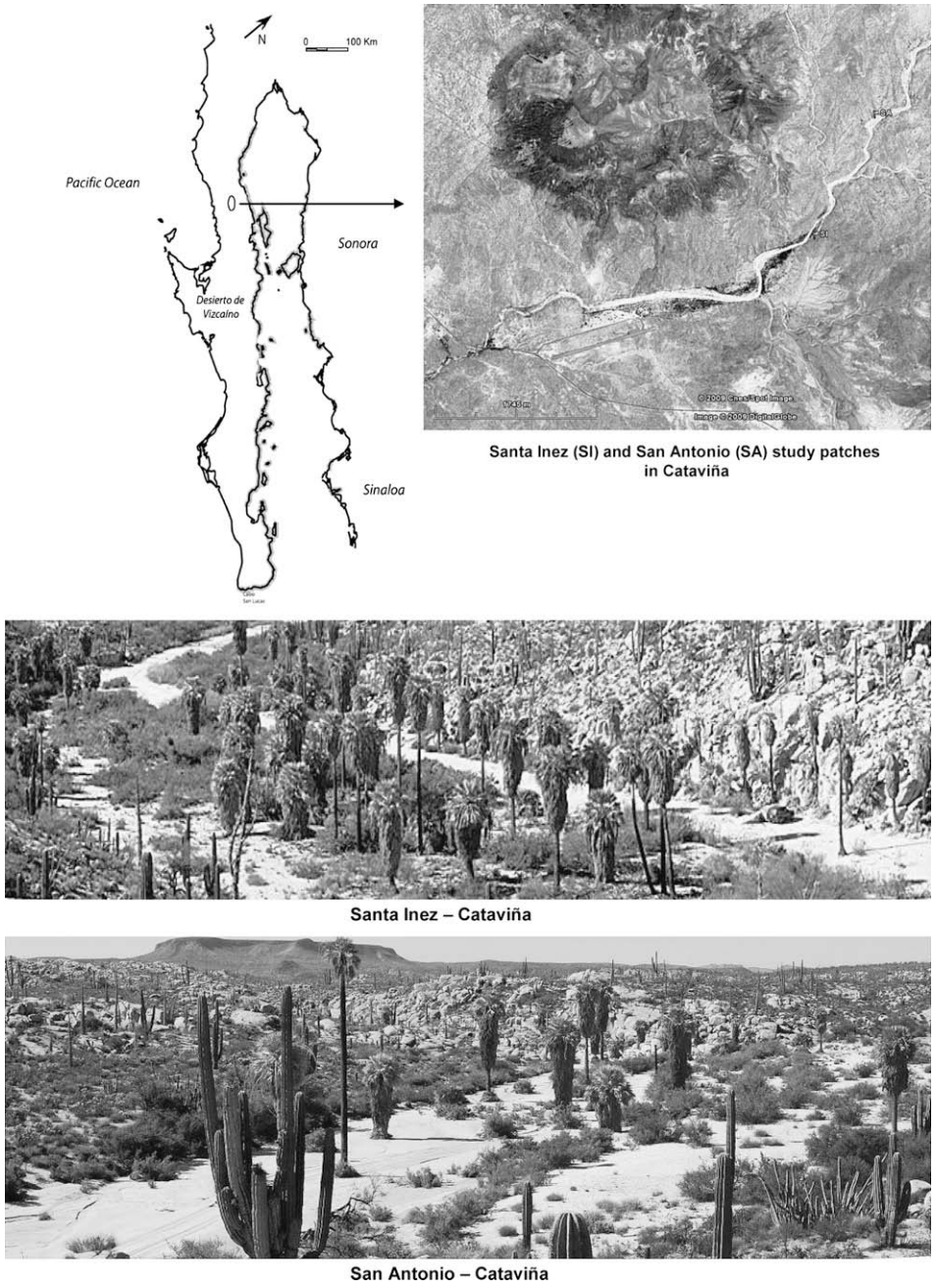

Fig. 1. Location of the Cataviña study area in Baja California, Mexico, and pictures of the two natural study palm patches, Santa Inez (SI) and San Antonio (SA).

$I_a > 1$, a spatially random variable has an $I_a = 1$, and a regular distributed variable has an $I_a < 1$. Counts were randomly arranged and the proportion of values in the frequency distribution that were as large as or larger than the observed value of D was calculated. Using a two-tailed test and $\alpha = 0.05$, a data set had an aggregated pattern if $p < 0.05$, a random pattern if p was between 0.05 and 0.95, and a regular pattern if $p > 0.95$.

The overall measure of spatial aggregation (I_a) is a good measure of the general spatial pattern of a data group, however it does not encompass all the facets of spatial pattern within an arrangement. Another index, the clustering index (v), quantifies the degree to which the count for each sample unit contributes to the overall degree of clustering, as a part of either a patch (areas with above-average density) or a gap (areas with below-average density). Thus, for example, for a donor unit i (sampling point with above-average abundance) having a flow of counts to n_j receiver units (sampling points with below-average abundance), the average distance of outflow is Y_i (see Perry et al., 1999). Then the SADIE procedure calculates an average outflow distance for each of the donor units. The value of Y_i is a good indicator of clustering, since it tends to be larger for a unit that is part of a patch than for one with an isolated large count and a relatively small number of neighbors. By convention, sampling points with large values of v_i (>1.5) are within-patches, and sampling points with large and negative values of v_j (<-1.5) are within gaps. Values close to unity indicate a random placement of that unit. Again, by employing randomizations in which the observed counts are permuted amongst the sample units, an index of clustering is ascribed to each sample unit. In these tests, the mean value of the clustering index over the patch units (V_i) and the mean value over the gap units (V_j) were compared

with an expectation of 1 and −1, respectively (their corresponding values for randomizations). The values of the clustering indices are continuous and may be mapped, interpolated and contoured, facilitating the identification and measurement of size, location and proximity to other clusters.

2.2.2. Spatial association between avian visits and availability of fruit

As a way to examine the strength of the relationship between fruit availability and avian frugivory, we evaluated the spatial relationships between these sets of counts sampled in identical times and locations (the index of clustering υ previously obtained) by using the SADIE spatial association method (Perry and Dixon, 2002). We obtained an overall spatial association index (X) (the simple correlation coefficient between the clustering indices of each set) and measures of local association (X_p) for each unit, which may then be mapped and contoured (Perry and Dixon, 2002). Assessments of the significance of X were tested against values of X_{rand} from randomization tests (we used 1000 randomizations in all analyses). Critical values and limits were estimated for X under the null hypothesis of no association, from centiles of the randomization distribution, X_{rand}. For a recommended two-tail test with say a size of 5% the probability level should be less than 0.025 for significant association or greater than 0.975 for significant dissociation. The significance of the randomization test was later corrected for the presence of small-scale spatial autocorrelation (Perry and Dixon, 2002) and each critical value inflated by a scale factor using the method of Dutilleul (1993). The process involves detrending each set if necessary and then calculating the corrected degrees of freedom for correlation. Thus we calculated an effective sample size that takes into account the degree of autocorrelation in the data. Large values of local association are indicated by the coincidence of a patch cluster for one set with a patch cluster for the other, or by the coincidence of two gaps; dissociation is indicated by a patch coinciding with a gap.

2.3. Seed predation patterns at focal trees

To evaluate seed predation activities by vertebrates and invertebrates around palm trees, eight and six focal palms were selected in the Santa Inez and San Antonio patches, respectively. The numbers of intact and predated seeds were counted in seven quadrats of 1-m^2 size per palm in September and November 2006. In order to evaluate if the intensities of seed predation by vertebrates and invertebrates were different below vs. away from the mother plant, three of these quadrats were randomly placed below palm crowns and four of them were placed at more than 3 m from the crown edges. Seeds predated by vertebrates were easily distinguished from those predated by invertebrates (Fig. 2c). In the former, teeth marks of rodents were easily noted, and in the latter, an exit hole was evident and the inside of seeds almost completely disintegrated or consumed. Based on our observations: 1) September was the peak of the fruiting season, when most of the fruits were more palatable for animals, and when a lot of seeds and fruits were found on the floor, 2) there might be differences in the availability of fruits and seeds between both study patches, and 3) there might be more aggregation of fruits and seeds below than away from palm trees. Therefore we explored if the total number of seeds predated differed between two times of the same fruiting season (September vs. November 2006), two patches (SI vs. SA), and two micro-environments (sites below the crown vs. sites at a distance >3 m away from crown edges), using Wilcoxon–Mann–Whitney tests. Then we evaluated if the intensity of seed predation by vertebrates and invertebrates differed between patches by using a Chi-square test of independence. Additionally, as a way to evaluate the significance of seed predation in blue fan palms, all quadrats were classified into four categories according to whether they contained seeds consumed by vertebrates (V), consumed by invertebrates (I), consumed by both predators (V + I), or left intact (no predation). We then evaluated if these categories were similarly or differently represented between patches, sample months and micro-environments, by using Chi-square tests of independence.

2.4. Seed dispersal activity at focal trees

As a measure of the intensity of the seed dispersal activity by mammals, we counted the number of feces containing blue fan palm seeds, in the same quadrats used before. Fecal samples were identified, measured and photographed to further confirm identities using the literature (Aranda, 2000; Ceballos and Oliva, 2005). We evaluated differences in the presence of feces between the two palm patches, two contrasting seasons (September 2006 and February 2007) and the two micro-environments respecting focal palms, by using Wilcoxon–Mann–Whitney tests. In order to determine the diversity and the evenness of feces found at each palm patch, we calculated the Shannon index of diversity (H') and the evenness (E) of mammal presence (Magurran, 1988). In these analyses we used a total of 42 quadrats and six focal trees per palm patch, in which we counted the number of feces per disperser species. We only used data from September 2006, the peak of the fruiting season, in these analyses. Diversity (H') and evenness (E), and their corresponding confidence limits and differences among palm patches, were obtained by using the Species Diversity and Richness III software, version 3.02 (Pisces Conservation Ltd., Lymington, Hants SO41 8GN, UK). The procedure evaluates statistical differences by performing a randomization test and recalculating each index with 10,000 random partitions (Solow, 1993). All other statistical analyses were performed with JMP software (version 3.2.2; SAS Institute, Inc. 1989–1997).

3. Results

3.1. Interactions between palms and the frugivore bird community

The quantity and phenological state of fruits, as well as avian visits, differed between plots; at both the within-patch and the patch scales (Table 1). At the within-patch (or individual tree) scale in Santa Inez, the quantity of fruits and avian visits showed highly significant clustering into patches and into gaps (Table 1). The phenological state of fruits also showed some degree of patchiness in this plot, although it was not statistically significant. At the same scale of the individual tree, San Antonio also showed some degree of aggregation of all variables, but they were not statistically significant, while the phenological state of fruits was significantly aggregated into patches (Table 1). When the variables were analyzed at the larger patch scale, Santa Inez still showed highly significant clustering of the quantity and the phenological state of fruits, as well as of bird visits (Table 1). However, San Antonio still showed statistically insignificant patterns of any of the variables considered; the mean clustering index was close to 1, a rather random pattern (Table 1). In Santa Inez the quantity and the phenological state of fruits showed significant spatial association with avian visits at both the patch and individual tree scales (Table 1). By contrast, in San Antonio, fruit variables were not significantly associated with avian visits, at either the patch or the individual tree scale (Table 1).

3.2. Seed predation activity at focal trees

The total number of seeds predated was higher in Santa Inez than in San Antonio ($\chi^2 = 25.5$, df = 1, $p < 0.0001$), and also greater

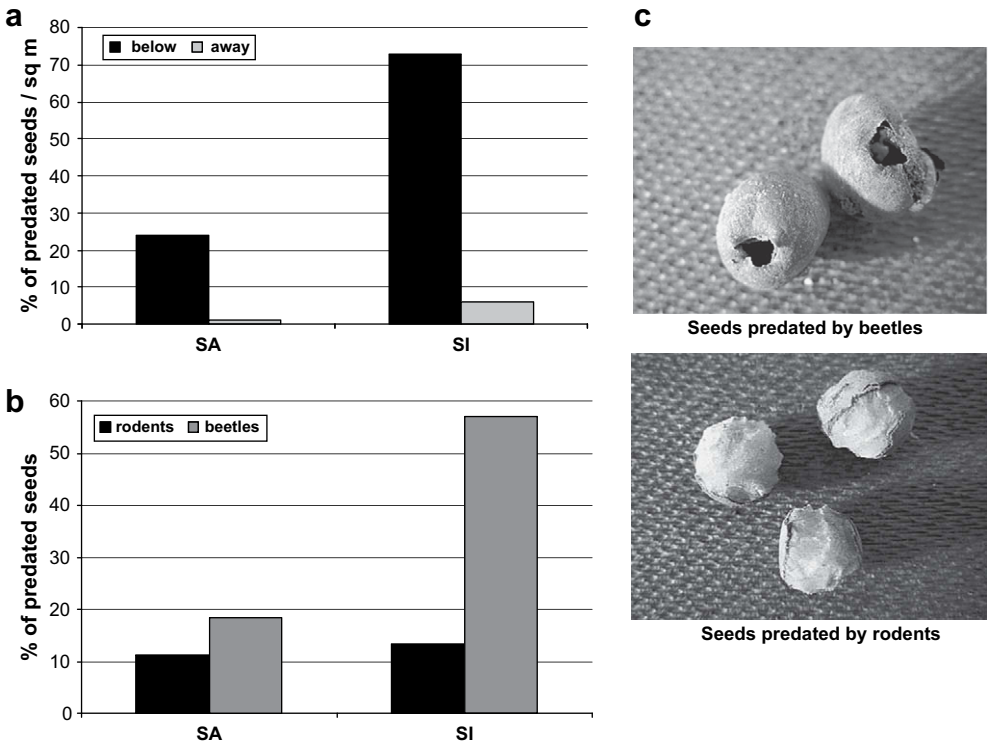

Fig. 2. Percentages of seeds predated per quadrats of 1 m^2 size: below the crown of palm trees (below), and at distances > 3 m from the crown limit (away) (a); and percentages of seeds predated by rodents and beetles (b), in the Santa Inez (SI) and San Antonio (SA) patches. c) Blue fan palm seeds showing contrasting patterns of predation by beetles and rodents.

below than away from palm trees ($\chi^2 = 56.5$, df = 1, $p < 0.0001$) (Fig. 2a), but it was similar between sampling times ($\chi^2 = 3.1$, df = 1, $p = 0.08$; $N_{\text{Santa Inez}} = 84$ and $N_{\text{San Antonio}} = 112$ quadrats). In Santa Inez, we found more seeds predated below palms than away from them (211 predated seeds in 36 quadrats below palms, vs. 22 predated seeds in 48 quadrats away, Fig. 2a). In San Antonio we also found more seeds predated below palms than away from them, but to a lesser degree than in Santa Inez (92 predated seeds in 48 quadrats below palms, vs. 6 predated seeds in 64 quadrats away, Fig. 2a). We observed that blue fan palm seeds were predated by rodents and beetles around and away from palms (Fig. 2c); therefore hereafter we will refer to beetles instead of invertebrates and to rodents instead of vertebrates. The intensity of seeds predated by rodents and beetles differed between patches ($\chi^2 = 12.7$, df = 1, 330, $p < 0.001$; Fig. 2b). In Santa Inez, 81% ($N = 233$) of seeds were predated by beetles, whereas in San Antonio this situation represented 62% of seeds ($N = 98$) (Fig. 2b). Quadrats with seeds predated by rodents (V), by beetles (I), by both predators (V + I), and by neither, differed between patches ($\chi^2 = 21.9$, df = 3, 193, $p < 0.0001$, Fig. 3a), and between microsites respecting the palms ($\chi^2 = 67$, df = 3, 193, $p < 0.0001$, Fig. 3b); but not between sampling times ($\chi^2 = 7.4$, df = 3, 193, $p = 0.06$). In Santa Inez, 53% of quadrats had seeds predated by beetles and/or rodents; however, in San Antonio most quadrats (78%) contained intact, unpredated seeds (Fig. 3a, c, d). At distances > 3 m away from palm trees, most quadrats presented intact seeds (85%); by contrast, 62% of quadrats below palms had predated seeds, and only 38% had intact seeds (Fig. 3b). One species of invertebrate, *Caryobruchus veseyi* Horn (Bruchidae), was observed to be responsible for a great proportion (76%, $N = 331$ seeds) of blue fan palm seed predation at the scale of individual palm trees in Cataviña. Below fan palms, adults of *C. veseyi* oviposit on seeds lying on the ground, and approximately 6 months later eggs hatched and adults emerged through an exit hole (Fig. 3d). Larvae are known to burrow and feed inside one or several seeds and then pupate inside the last one predated (Nilsson and Johnson, 1993). Another beetle species, *Eusattus catavinus* Doyen (Tenebrionidae), was also collected in Cataviña. These beetles inhabit the sandy canyon bottom, where they aggregate in the litter beneath the canopies of shrubs (M. Wall, personal communication), however they were not seen ovipositing on blue fan palm seeds.

Table 1
SADIE indices and probabilities (p) of the quantity of fruits (fruit qty), the phenological phase of fruits (fruit phph), and the number of avian visits in 10 min intervals (avian visits) in two study plots (Santa Inez and San Antonio) of the Cataviña area. See text for details of variable estimations. I_a: index of aggregation, n: total number counted, X: overall index of association of fruit qty and phph with avian visits. In bold: significant spatial aggregation and spatial association index.

Scale of study	Study plots (5 m × 5 m unit size)	Variable	I_a (p)	N	X (p)
Within-patch (0.2 ha)	Santa Inez	Fruit qty	**1.96 (0.01)**	66	**0.5 (<0.01)**
		Fruit phph	1.4 (0.11)		**0.6 (<0.0001)**
		Avian visits	**2.5 (0.001)**		
	San Antonio	Fruit qty	1.3 (0.2)	29	0.1 (0.3)
		Fruit phph	1.5 (0.1)		0.3 (0.1)
		Avian visits	1.2 (0.2)		
Patch (approx. 2 ha)	Santa Inez (1.9 ha)	Fruit qty	**2.4 (<0.001)**	752	**0.4 (<0.01)**
		Fruit phph	**2.4 (<0.001)**		**0.4 (<0.01)**
		Avian visits	**2.9 (<0.001)**		
	San Antonio (3.1 ha)	Fruit qty	0.9 (0.6)	1227	0.3 (0.1)
		Fruit phph	0.9 (0.6)		0.3 (0.1)
		Avian visits	1.1 (0.3)		

3.3. Seed dispersal activity at focal trees

The presence of seed dispersers' feces was similar between the two palm patches in Cataviña ($\chi^2 = 1.9$, df = 1, $p = 0.2$; $N_{SI} = 84$,

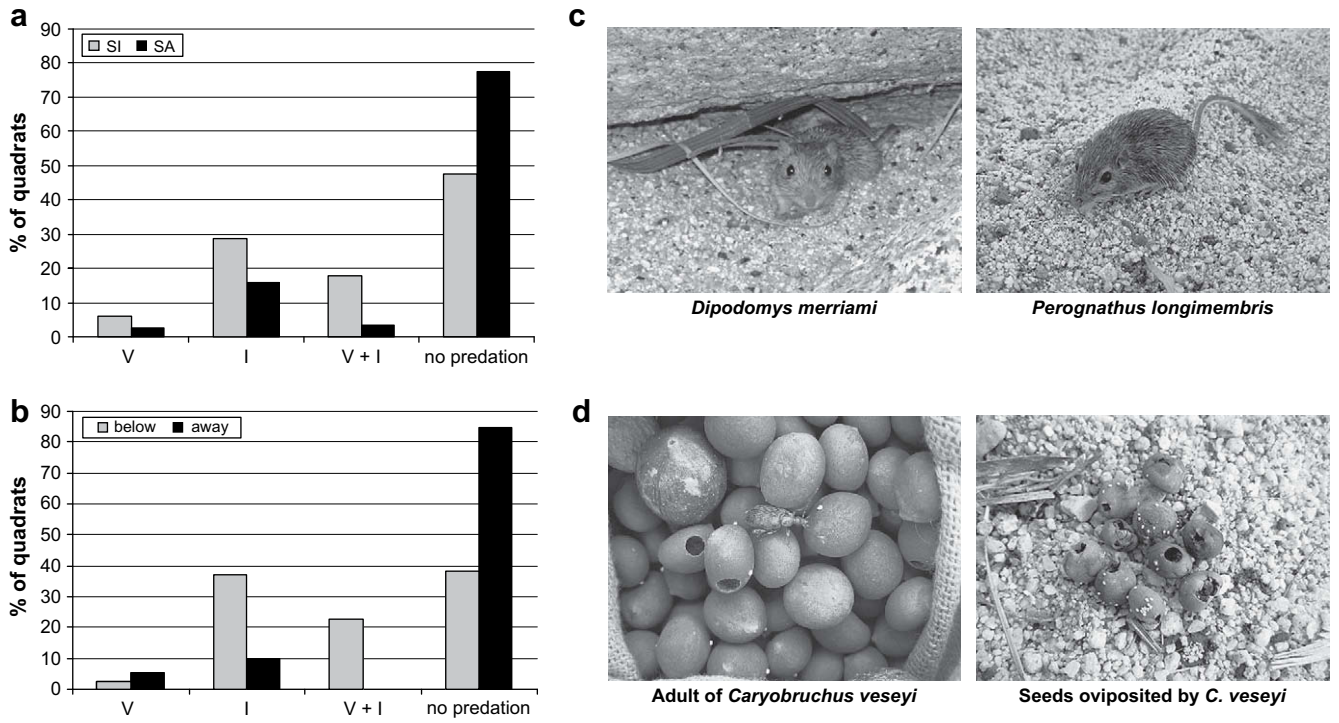

Fig. 3. Percentage of quadrats with seeds predated by rodents (V), seeds predated by beetles (I), seeds predated by both predators (V + I), and without seed predation (no predation): a) per study patch: Santa Inez (SI), and San Antonio (SA); and b) per microsites respecting the palms: below the crown (below), and at distances > 3 m from the crown limit (away). c) Common rodent seed predators observed during the study period, d) adult *Caryobruchus veseyi* and oviposited seeds.

$N_{SA} = 112$ quadrats), while more feces were found below palm crowns than >3 m away from palm crowns ($\chi^2 = 8.4$, df = 1, $p = 0.04$), and more during September than February ($\chi^2 = 11.1$, df = 1, $p = 0.0009$). From a total of 836 feces containing blue fan palm seeds collected during both seasons and plots, 525 (63%) corresponded to September and 311 (37%) to February. From a total of 525 feces collected during September (the peak of the fruiting season), similar numbers, 45% and 55%, corresponded to Santa Inez and San Antonio, respectively. Results from randomization tests showed that diversity and evenness of feces were significantly greater in the San Antonio patch ($H' = 1.76$, lower and upper 95% confidence limits of randomization distributions: 1.54–1.86; $E = 0.85$, lower and upper 95% confidence limits of randomization distributions: 0.80–0.95) than in the Santa Inez patch ($H' = 1.05$, lower and upper 95% confidence limits of randomization distributions: 0.95–1.13; $E = 0.58$, lower and upper 95% confidence limits of randomization distributions: 0.55–0.74) ($p < 0.0001$ for H' and E).

4. Discussion

4.1. Interactions between palms and the frugivore bird community

The bird community in Cataviña responded to fruit aggregation not only at the individual tree scale, but also at larger patches of 2 ha size. This was evidenced by relating bird activities with the quantity and phenological state of palm fruits between patches that differed in the degree of aggregation of these variables. When fruit variables were not aggregated (as they were in SA), birds responded to this pattern, showing no aggregation of their activities, and this occurred both at the scale of individual trees and at the patch level of 2 ha size. However, when fruit variables were aggregated (as in SI), birds responded by showing aggregation of their activities at both spatial scales. The way in which animals responded to fruiting patterns and spatial heterogeneity at different scales of the dominant vegetation is relevant particularly in areas that depend on uncertain climatic events, as the frequency of such events is expected to change in the face of future climatic fluctuations. Dominant plants provide not only food, water and habitat for a great number of animals, but also ecosystem structure, so any changes in patterns and processes can be expected to have cascading effects on the entire ecosystem, with considerable conservation implications. The concordance of patterns among successive spatial scales may be translated as similarities in foraging behavioral responses to the spatial aggregation of fruits at both study scales, the individual tree and the natural patch scale. As a consequence, seed dispersal may have homogeneous effects in palm population dynamics at both scales, at least for those palm seeds that can be transported some distance away from high seed mortality areas near the parent plants by large birds like ravens, jays and woodpeckers. However, when the patterns are concordant, it is difficult to clearly relate scale-specific patterns to processes and mechanisms occurring at the same scale. Other studies also found that frugivores were able to cope with spatial heterogeneity of fruit-resource availability at different scale parameters (García and Ortiz-Pulido, 2004), but patterns were found to be discordant among scales. Further studies may classify and separate birds according to their range of action (resident or migratory) and probably show different activity patterns in response to fruit aggregation. Consequently, they would suggest heterogeneous effects of birds' role as seed dispersers on palm population dynamics.

Because palm fruits and seeds are critical as food and water resources for many animals in this type of environment, most animals visiting infructescences are likely to act as predators, even though they are sometimes acting or referred to as dispersers (Henderson, 2002). In Cataviña, 32 bird species were registered during the period of study, from which 56% were year-round residents, 16% were occasional visitors to the oasis during the breeding season, and 28% were winter residents (Appendix A). Visits of bird species were more or less evenly distributed during the period of

study; *Icterus cucullatus* constituted 28% of total visits ($N = 231$), followed by *Melanerpes uropygialis* (19%), *Spizella breweri* (17%), *Callipepla californica* (9%) and *Corvus corax* (6%) (Appendix B). This highlights the critical importance of isolated oases to resident birds, as well as breeding and wintering residents, and their significance as stopover sites for migrating birds. Other studies support these findings by showing the importance of riparian corridors regardless of their size and degree of isolation or connectivity (Bairlein, 1988, 1992; Biebach, 1990; Skagen et al., 1998). Some bird species have great mobility over relatively large distances and probably are able to use landscape cues to efficiently track fruit availability along canyons within a region. In general, resident birds scarcely fly over long distances but are very efficient in using isolated large crop-size palms as 'stepping stones' among local patches, concentrating in rich-fruited individual plants (Fischer and Lindenmayer, 2002). The mechanisms behind the fruit-resource tracking at different scales (grain and scale concepts following Turner, 1989) could be explored in the frugivore behavioral response to resource heterogeneity (Sallabanks, 1993). As in Sallabanks (1993), here we found that birds were able to track fruiting palms at the individual tree level as well as when fruits were aggregated in larger patches, and this pattern probably reflects a hierarchical system of decision-making for frugivorous birds. From the palm point of view, scaling palm–frugivore interactions in these oases is relevant since the ecological and evolutionary outcomes of palm seed dispersal may depend on the spatial and temporal scales at which frugivory patterns arise.

4.2. Seed predation activity at focal trees

In San Antonio plot we found fewer predated seeds per square meter than in Santa Inez. San Antonio was the farthest from the main road and near the most commonly used path by off-road tourism and cattle. In contrast, the Santa Inez site was less frequently visited by tourists and occasionally used by cattle seeking shade under palm trees. We suggest that predation differences might be explained by differences in the levels of anthropogenic alteration between plots. However, other causes might have influenced the differences evidenced in the seed predation activity pattern. The physiography of the canyons in Cataviña was different from the San Antonio site, which is a very wide canyon without much coverage of understory plants and/or rocks. This fact may limit rodents from hiding places and make them more susceptible to natural predators. Such an effect has the potential to restrict rodent movement patterns, and consequently seed removal activities. On the other hand, results from spatial patterns of frugivory activity by birds showed that palm fruits in San Antonio were more sparsely distributed than in Santa Inez. This is in accordance with the higher seed predation values found below palms in Santa Inez than in the San Antonio plot; most of this predation activity corresponded to beetles that attacked seeds due to the high fruit and seed concentrations below trees. Therefore, predation differences among plots might also be explained by differences in resource aggregation among them; palm trees in San Antonio were more sparsely distributed than in Santa Inez (Fig. 1). Since rodents were able to remove seeds from these sites, we were probably underestimating real rodent seed predation and/or dispersal rates. Seed predation did not differ between the two sampling times, suggesting homogeneous predation pressures at least during a lapse of two months in these canyons.

4.3. Seed dispersal activity at focal trees

The intensity of dispersal by vertebrates was higher below palms than farther away, but it was similar between Santa Inez and San Antonio; however the diversity of feces was greater in San Antonio than in Santa Inez during the study period. Also high values of evenness were registered for San Antonio, indicating that disperser species were evenly represented in this plot. Most fecal samples collected corresponded to coyotes, grey and desert foxes, and lynxes; however, signs of the presence of pumas, ring tails, raccoons, spotted skunks and badgers were also registered in these canyons (Plate 1, Suppl. data). All of them function as seed dispersers, taking seeds throughout canyons and between patches. Considering that the Cataviña study area occupied approximately 1.2 km^2 and that estimations of home-range sizes of potential dispersers matched and even exceed this area (coyote: 9–90 km^2, Laundré and Keller (1984); grey fox: approx. 5 km^2, Swihart et al. (1988); spotted skunk: 0.7 km^2, Jones et al. (1985); puma: 26–760 km^2, Grigione et al. (2002); lynx: 31–96 km^2, Litvaitis et al. (1986); raven: 2.8–45.8 km^2, Linz et al. (1992)), we feel confident to suggest that these animals use canyons as corridors, bringing seeds from other palm populations located several kilometers away. The quantity of fecal samples varied among the two sampling times; it was greater at the peak of the fruiting season, when fruits were more palatable to animals, than two months later, when the fruits were old and dry. It is at this period when endozoochorous seed dispersal by animals of blue fan palm seeds acquires great importance for these ecosystems.

The vector which was probably responsible for relocating most viable seeds was the pulses of overland water flows which transported seeds downhill and eventually determined the pattern of adult distributions we currently see along drainage lines. Nevertheless, not all blue fan palms were distributed in this way; endozoochorous seed dispersal was evident in this study, especially at the peak of fruiting seasons. Since seed dispersal in desert canyons may be mainly governed by episodic events of winds and water flows through landforms and topography, the estimation of the qualitative and quantitative importance of palm seed dispersal by animals is relevant to start understanding 'multidirectional' (as opposed to 'unidirectional') forces of dispersal that may influence the occurrence and maintenance of this desert riparian ecosystem. Palms commonly seen growing from crevices on cliffs indicate that dispersal must also take place uphill. As the ancient megafauna that inhabited and very probably, had close relationships with palm species similar to blue fan palms more than two million years ago, today several vertebrate seed dispersers also travel along ridgelines crossing diverse canyons and transporting blue fan palm seeds to sites where predation rates would be relatively low. Among them, ravens, jays, pumas, lynxes, coyotes, foxes, bighorn sheep (*Ovis canadensis*) and mule deer (*Odocoileus hemionus*) have been observed to use canyons as sources of water and food, taking seeds in their movements from lowlands to uplands and connecting isolated palm populations. The importance of processes acting at small scales cannot be excluded, since significant beetle predation was detected below the palms. Since blue fan palms may attain supracentenarian longevity (Bullock and Heath, 2006), current observations on processes in the recent history of oasis ecosystems may not yield representative conclusions about the factors that determined adult palm distributions. However, such studies are critical in revealing present ecological interactions and are essential to start understanding future changes of this key sustaining ecosystem in the northern desert region of the peninsula.

Results showed that blue fan palms function as important sources of fruits, seeds and shelter for a great number of animals at the individual tree level. In turn, palm trees are aggregated in patches along canyons with water and other resources, which constitute corridors for animals and endozoochorously dispersed

seeds. Such riparian ecosystems embedded in arid environments influence human and nonhuman life, providing fundamental ecological services, regulating water regimes, and acting as sources of biodiversity. The values of these functions to human society depend on a complex set of relationships between oases and the surrounding environment. Efforts directed toward the sustainable management of these critically endangered ecosystems are crucial, and difficult decisions will need to be made about ecological sustainability and management. The increase in world population and the importance of water for human development will work against effective conservation of wetlands in deserts. Since measurements of the frequency or magnitude of such degradation have not been attempted to any significant degree, an important challenge for conservation in deserts will be the understanding of their oasis ecosystem dynamics.

Acknowledgements

This research was funded by the Institute of International Education and the Alcoa Foundation fellowship awarded to E.W., and by The David and Lucile Packard Foundation granted to E.E. We greatly appreciate the support of the BRCC at the San Diego Natural History Museum and of Joe Perry, who provided us with a larger version of SADIE software. We want to thank Víctor Sánchez Sotomayor, the director of the Valle de los Cirios Natural Protected Area, for his support and the authorization to do research in the Protected Area, and Michael Wall at the San Diego Natural History Museum for kindly identifying the beetles collected. We are grateful to Nils Jacobson who kindly reviewed the last version of this manuscript and Pablo Jorgensen for his help in the field.

Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jaridenv.2009.03.007.

Appendix A

List of 32 total bird species registered in the Cataviña area which do or do not eat blue fan palm fruits. NOM: National Endangered Species List (NOM-059, SEMARNAT 2001), Pr: Special protection category; IUCN: Red List (NT: near threatened, LC: list concern).

Bird species	Diet	Habitat range	NOM	IUCN
Aeronautes saxatalis	Insects, fruits, seeds, nestling birds, reptiles, amphibians, carrion	Resident	–	LC
Amphispiza bilineata	Seeds	Resident	–	LC
Callipepla californica	Seeds, fruits, insects, small vertebrates	Resident	–	LC
Carduelis psaltria	Seeds, fruits, insects	Resident	–	LC
Carpodacus mexicanus	Seeds, insects, fruits	Resident	–	LC
Colaptes chrysoides	Insects, fruits	Resident	–	LC
Contopus sp.	Insects	Breeding	–	LC
Corvus corax	Omnivorous	Resident	–	LC
Dendroica petechia	Insects, fruits	Breeding	–	LC
Empidonomus varius	Insects	Resident	–	LC
Geococcyx californianus	Insects, reptiles, fruits, small mammals, eggs	Resident	–	LC
Icterus cucullatus	Fruits, nectar	Winter	–	LC
Icterus parisorum	Fruits, nectar	Winter	–	LC
Icterus wagleri	Fruits, nectar	Winter	Pr	LC
Lanius ludovicianus	Mice, insects, small birds	Resident	–	LC
Melanerpes uropygialis	Insects, fruits	Resident	–	LC
Phainopepla nitens	Insects, fruits	Resident	–	LC
Pheucticus chrysopeplus	Seeds, fruits	Breeding	–	LC
Pheucticus melanocephalus	Seeds, fruits	Breeding	–	LC
Picoides villosus	Insects, fruits	Resident	–	LC
Pipilo crissalis	Seeds, insects	Resident	–	LC
Piranga ludoviciana	Seeds, fruits, insects	Breeding	–	LC
Polioptila melanura	Insects, fruits	Resident	–	LC
Psaltriparus minimus	Insects	Resident	–	LC
Sayornis nigricans	Insects	Resident	–	LC
Spizella breweri	Seeds, insects	Winter	–	NT
Troglodytes aedon	Insects	Winter	–	LC
Turdus migratorius	Insects, fruits	Winter	–	LC
Tyrannus vociferans	Insects	Winter	–	LC
Wilsonia pusilla	Insects, fruits	Winter	–	LC
Zenaida asiatica	Fruits, seeds, flowers, leaves and invertebrates	Resident	–	LC
Zonotrichia leucophrys	Seeds, insects	Winter	–	LC

Appendix B

List of 321 total and percentages bird visits in 10-min bouts observed eating blue fan palm fruits during the period of study in the Cataviña oasis. The most frequent visitors are shown in bold.

Bird species	Visits in 10′	% Of visits
Callipepla californica	**21**	**9.09**
Carduelis psaltria	2	0.87
Carpodacus mexicanus	4	1.73
Carpodacus purpureus	3	1.30
Colaptes chrysoides	1	0.43
Corvus corax	14	6.06
Dendroica petechia	1	0.43
Icterus cucullatus	**65**	**28.14**
Icterus parisorum	12	5.19
Melanerpes uropygialis	**44**	**19.05**
Phainopepla nitens	1	0.43
Pheucticus chrysopeplus	1	0.43
Pheucticus melanocephalus	6	2.60
Picoides villosus	4	1.73
Pipilo crissalis	3	1.30
Piranga ludoviciana	1	0.43
Sayornis nigricans	1	0.43
Spizella breweri	**40**	**17.32**
Troglodytes aedon	1	0.43
Tyrannus vociferans	1	0.43
Zenaida asiatica	3	1.30
Zonotrichia leucophrys	2	0.87
Total of visits	**231**	

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