

Relationships between El Niño Southern Oscillation and Demographic Patterns in a Substitute Food for Collared Peccaries in Panama¹

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ABSTRACT

Environmental fluctuations can play an important role in shaping demographic processes in plant and animal populations. On Barro Colorado Island (BCI), Panama, El Niño Southern Oscillation (ENSO) events followed by mild dry seasons have been shown to stimulate variation in community-wide fruit production. This variation has been postulated to lead to famine in frugivore and granivore populations, but few if any studies have assessed further implications for other members of the ecological community. This study examined the ways in which variation in fruit production associated with an El Niño event on BCI may influence demographic and evolutionary traits in a plant species that is only consumed by frugivores during periods of fruit scarcity. Specifically, I assessed the effects of herbivory by collared peccaries (*Tayassu tajacu*) on demographic rates and patterns in the terrestrial bromeliad, *Aechmea magdalenae*. *Aechmea magdalenae* usually suffers little or no herbivory, and rain forest collared peccaries, which are primarily frugivorous, have not previously been reported to eat this species. Rates of survival and reproduction of 296 *A. magdalenae* rosettes in three transects of differing densities were recorded from 1997 through 1999. Mortality rates due to herbivory increased significantly from 1997 to 1999 and showed a close correspondence with enhanced and then decreased rates of community-wide fruit production associated with the 1997 ENSO. The densest portions of the *A. magdalenae* population showed lower mortality rates and higher rates of reproduction than did the less dense regions. Over the study period, *A. magdalenae* populations decreased by 45 percent. The implications of periodic herbivory by hungry frugivores are discussed with respect to population regulation, seedling dispersal, and evolution of *A. magdalenae*'s dense growth habit.

RESUMEN

Se reconoce que las fluctuaciones climáticas juegan un papel importante en los procesos demográficos de las poblaciones de plantas y animales. En la isla Barro Colorado (BCI), Panamá, los fenómenos El Niño/Oscilación del Sur (ENOS), seguidos de períodos moderadamente secos, han producido variación en la producción de frutos a nivel de comunidades vegetales. Se ha propuesto que esta variación se asocia con las épocas de hambruna de las poblaciones de frugívoros y granívoros, pero hasta donde se sabe, ningún estudio ha investigado su impacto en otros miembros de la comunidad ecológica. Este estudio examina las formas en que la variación en la producción de frutos asociada con ENOS, puede influir las características evolutivas y demográficas de una especie vegetal que sólo es consumida por frugívoros durante períodos de baja producción de frutos. Específicamente, se examinan los efectos que la herbivoría por pecarí de collar (*Tayassu tajacu*) tiene sobre las tasas y patrones demográficos de la bromelia terrestre *Aechmea magdalenae*. *Aechmea magdalenae* usualmente padece poca herbivoría, y no existen reportes de pecaríes de collar alimentándose de ella. Entre 1997 y 1999 se registraron las tasas de supervivencia y reproducción de 296 rosetas de *A. magdalenae* en tres transectos con diferente densidad de rosetas. Las tasas de mortalidad debidas a la herbivoría se incrementaron significativamente en este período y mostraron una estrecha correspondencia con las tasas decrecientes en la producción de frutos de la comunidad asociadas con el ENOS de 1997. Los transectos con mayor densidad de *A. magdalenae* mostraron tasas de mortalidad más bajas y tasas de reproducción más altas respecto a los transectos de menor densidad. A lo largo de todo el período del estudio, las poblaciones de *A. magdalenae* decrecieron un 45 por ciento. Las implicaciones que ocasiona la herbivoría periódica por frugívoros hambrientos se discute en relación con la regulación de la población, dispersión de semillas, y evolución de los hábitos de crecimiento de *A. magdalenae*.

Key words: *Aechmea magdalenae*; Barro Colorado Island; collared peccaries; El Niño Southern Oscillation; herbivory; *Tayassu tajacu*; temporal variation.

THE IMPORTANCE OF ENVIRONMENTAL FLUCTUATIONS IN SHAPING DEMOGRAPHIC PROCESSES is well recog-

nized. Interannual variation in environmental conditions can affect rates of growth, reproduction, and mortality of plants (Menges 1992, Horvitz & Schemske 1995, Nations & Boyce 1997) and animals (Langvatn *et al.* 1996, Siriwardena *et al.*

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1999, Lima *et al.* 2001), and may do so by altering plant–animal interactions (Bastrenta 1995, Ehrlen 1995, Palmisano & Fox 1997, Piqueras 1999).

The El Niño Southern Oscillation (ENSO) is the major cause of interannual climatic variation in the tropics and has been shown to influence demographic patterns in plants and animals. For example, mast fruiting by Dipterocarpaceae in Southeast Asia is believed to be triggered by ENSO events (Ashton *et al.* 1988, Curran *et al.* 1999, Yasuda *et al.* 1999). On Barro Colorado Island (BCI) in Panama, the tendency for ENSO to produce dry, sunny years followed by wet, cloudy years (Aceituno 1998) alternately enhances and reduces forest-wide fruit production (Wright *et al.* 1999). Wright *et al.* (1999) showed that enhanced fruit production during El Niño events may maintain frugivore populations at elevated densities on BCI. Moreover, they presented evidence that this can exacerbate a frugivore famine if the following year had a mild dry season, low insolation, and most importantly, very low community-level fruit production. Over a 49-year record on BCI, frugivorous mammals are thought to have experienced famine and high mortality every time an El Niño event was followed by a mild dry season (Wright *et al.* 1999).

Although variable fruit production associated with some El Niño events may also hold demographic implications for other members of the ecological community, few if any studies have considered this issue. For example, decreased levels of fruit production may lead to increased levels of herbivory on plant species that are consumed by frugivores only in times of fruit scarcity. This may result in selective pressures on these substitute foods that are not apparent during most years. Assessing the effects of infrequent but periodic events on the demography of these species can therefore be fundamental to understanding their ecology and evolution.

This study examined some of the ways in which environmental fluctuations associated with an El Niño event may influence demographic and evolutionary patterns in a plant species that is only consumed during periods of decreased community-wide fruit production. Specifically, I assessed the effects of herbivory by collared peccaries (*Tayassu tajacu*) on demographic rates and patterns in the terrestrial bromeliad *Aechmea magdalenae* from 1997 through 1999 on BCI. The 1997 El Niño conditions on BCI resulted in the highest level of community-wide fruit production recorded since fruit production records started in 1987. Fruit pro-

duction then dropped to well below average levels during the following two years (Wright *et al.*, pers. comm.), both of which had above average levels of precipitation during the dry seasons (Paton 1998, 1999). Collared peccaries are primarily frugivorous in rain forest environments (Kiltie 1981) and are reported to have suffered famines on BCI every time an El Niño event was followed by a mild dry season (Wright *et al.* 1999). *Aechmea magdalenae* has been reported to experience little or no herbivory (Brokaw 1983) and herbivory by collared peccaries has not previously been recorded for this species. *Aechmea magdalenae* rosettes propagate vegetatively to form extremely dense patches of all sizes, although rosettes show negative density-dependent growth (Ticktin *et al.* 2003).

My objectives were to quantify rates and patterns of recruitment and mortality in *A. magdalenae* and to examine their relationships to herbivory by peccaries and levels of community-wide fruit production during and after the 1997 ENSO event. I also assessed if periodic herbivory by peccaries may exert selective pressures on *A. magdalenae* populations for a dense growth habit by comparing rates of herbivory, mortality, and recruitment among *A. magdalenae* transects of differing densities.

STUDY SITE AND SPECIES

Barro Colorado Island (BCI) is located in the Panama Canal (9°9'N, 79°51'W) and was created when Gatun Lake was flooded to create the canal. It supports tropical moist rain forest with a 35 m tall canopy and has an annual average rainfall of 2600 mm. There is a dry season that extends from December to April.

Aechmea magdalenae is a long-lived, terrestrial, understory bromeliad, with long, spiny, fibrous leaves that grow to 3 m in length. It is found in dense and usually monospecific patches along streams, in swampy areas, and on hillsides in humid Neotropical rain forests from Mexico to Ecuador (Croat 1978). *Aechmea magdalenae* rosettes sit on a thick, succulent horizontal meristem, part of which lies under the soil. Rosettes commonly propagate vegetatively through rhizomes, which produce a single ramet at the tip. *Aechmea magdalenae* is monocarpic and seedlings are rarely found in nature (Brokaw 1983, Villegas 2001; Ticktin, pers. obs.).

METHODS

In early November 1997, three permanent transects were established in one extensive *A. magdalenae*

TABLE 1. *Density and decrease in population size of A. magdalenae rosette in three transects from 1997 to 1999 on Barro Colorado Island.*

Transect	Average density (rosettes/m ²)		Proportion of rosettes >180 cm		Population decrease 1997– 1999 (%)
	1997	1998	1997	1998	
1	1.7	1.1	60.2	67.2	37.5
2	1.3	0.95	44.2	52.2	47.9
3	1.1	0.93	34.3	42.9	59

population located at the end of Zetek trail on BCI. This population extends for more than 200 m on both sides of the trail. All rosettes falling within the transects, which ranged in size from 14 to 19 m long \times 5 m wide, were labeled with aluminum tags and monitored annually in November for survival, growth, vegetative propagation, and sexual reproduction over a period of three years (1997–1999). Initial number of rosettes was 98, 98, and 100 in transects 1, 2, and 3, respectively, for an initial total of 296 rosettes.

The three transects varied in rosette density and in stage structure (Table 1). Transect 1 had the highest density, with the greatest number of rosettes per square meter as well as the highest proportion of rosettes in the largest stage classes. Transect 3 was the least dense with respect to both of these measures.

Herbivory by peccaries was recorded during the months of November and March through observations of peccaries digging up and eating the stems of *A. magdalenae* rosettes, and by the presence of dead rosettes that had their stems eaten. *Aechmea magdalenae* mortality by peccaries is easily identifiable because peccaries dig up the rosette, eat the succulent underground portion of the stem, and leave the stemless rosette lying on its side. *Aechmea magdalenae*'s fibrous leaves are very slow to disintegrate and dead, labeled rosettes can remain on the forest floor for several months. All reported ENSO-related frugivore famines on BCI have occurred between September and January (Wright *et al.* 1999), when fruit production on BCI tends to be at its lowest and death rates of frugivorous mammals are at their highest (Milton 1990, Wright *et al.* 1999). By monitoring *A. magdalenae* populations each year in November, I was therefore able to record herbivory when it was likely at its highest. Although I observed no herbivory by any other mammals, I cannot rule out the possibility that

rosettes may also have been eaten by other frugivores such as coati (*Nasua nasua*).

To assess size-specific mortality rates due to peccary predation, I divided the rosettes into stage classes that were previously defined from demographic analyses. These stage classes were separated according to both life history stage and size because vital rates were found to vary with both variables. Size was estimated by measuring rosette width since this was the best predictor of total leaf area ($R^2 = 0.84$, $N = 40$). Within life history stages, the stage classes were divided according to the algorithm proposed by Vandermeer (1978), which minimizes both sample and distribution errors. These stage classes were: (1) <40 cm, (2) 40–80 cm, (3) 80–180 cm, (4) 180–280 cm, and (5) >280 cm. Rosettes in stage classes 1–2 do not reproduce vegetatively or sexually, and rosettes in stage classes 3–5 are capable of vegetative propagation. Flowering and fruiting rosettes were excluded from analyses of mortality rates since all rosettes die after flowering in this monocarpic species.

Differences in *A. magdalenae* mortality and recruitment rates between years were tested using repeated measures ANOVA. For these analyses, year was considered to be the repeated factor and the three transects were considered replicates. Analyses were run for each stage class separately as well as for all stage classes together. Rates of recruitment due to vegetative propagation were obtained by dividing the number of ramets produced and surviving after one year by the number of vegetatively propagating rosettes (stage classes 3 and above). Likewise, the rate of recruitment by meristematic portions of dead rosettes was calculated by dividing the the number of ramets that produced from dead rosettes and that were surviving after one year by the number of dead rosettes. Seedling recruitment was computed as the number of seedlings per flowering rosette that germinated and survived after one year.

To test if trampling by peccaries or other animals had an effect on seedling survival, I used contingency analysis to compare germination and survival of seeds planted inside and outside of four exclosures over a one-year period. Exclosures were made of galvanized wire cloth and were 1 m tall \times 0.75 m diameter. They were placed randomly within the *Aechmea* Zetek population but outside of the transects. For two exclosures, I planted 55 seeds inside and 55 seeds outside the exclosure, and for the other two exclosures, I planted 35 seeds inside and the same number outside. The exclosures were not closed on top so that they protected seeds from

trampling but not from leaf litter. They were staked firmly to the soil to prevent the passage of mammals underneath.

RESULTS

Herbivory by collared peccaries resulted in a large decrease in the size of the *A. magdalenae* population. The total number of *A. magdalenae* rosettes in the transects decreased by 25 percent from 1997 to 1998, and by another 27 percent from 1998 to 1999. At the end of 1999, the monitored *A. magdalenae* population was only 45 percent of its original size (Fig. 1).

RATES AND PATTERNS OF MORTALITY.—Peccaries ate *A. magdalenae* rosettes in the smaller stage classes first and then moved on to the larger stage classes (Fig. 1). At the time of the first census, November 1997, there was no evidence of herbivory by peccaries in any *A. magdalenae* rosettes, inside or outside of the transects. One year later, I observed evidence of herbivory in the first three stage classes only. By 1999, peccary herbivory of rosettes in all stage classes was readily apparent. There were significant increases in mortality rates between years for all stage classes except stage class 2 (Table 2). Stage class 2 showed increased rates of mortality over time in transects 1 and 2, but in transect 3, the already elevated rate of mortality (*ca* 70%) remained stable (Fig. 2).

When the repeated measures analysis was run with all stage classes together, the stage class \times time interaction was significant ($df_{4, 10}$, $F = 9.20$, $P < 0.002$), indicating that rates of herbivory changed over time in different ways for the different stage classes. Overall mortality rates increased significantly over time ($df_{1, 10}$, $F = 88.47$, $P < 0.001$) and from 1997 to 1999, there were large decreases in the number of rosettes in all stage classes. Only the number of ramets produced from dead mother rosettes increased over time. Note that these ramets are illustrated as a subdivision of stage class 1 in Figure 1 because they tend to show greatly reduced rates of growth and significantly higher rates of mortality than ramets produced from live mother rosettes (Ticktin *et al.* 2003).

Mortality rates of rosettes in different stage classes varied greatly among the three transects of differing densities (Fig. 2). At the time of the second census (November 1998), I found evidence of peccary predation for rosettes in stage classes 1 and 2 in all transects, but only for rosettes in stage class 3 in transect 3, which was the least dense of the

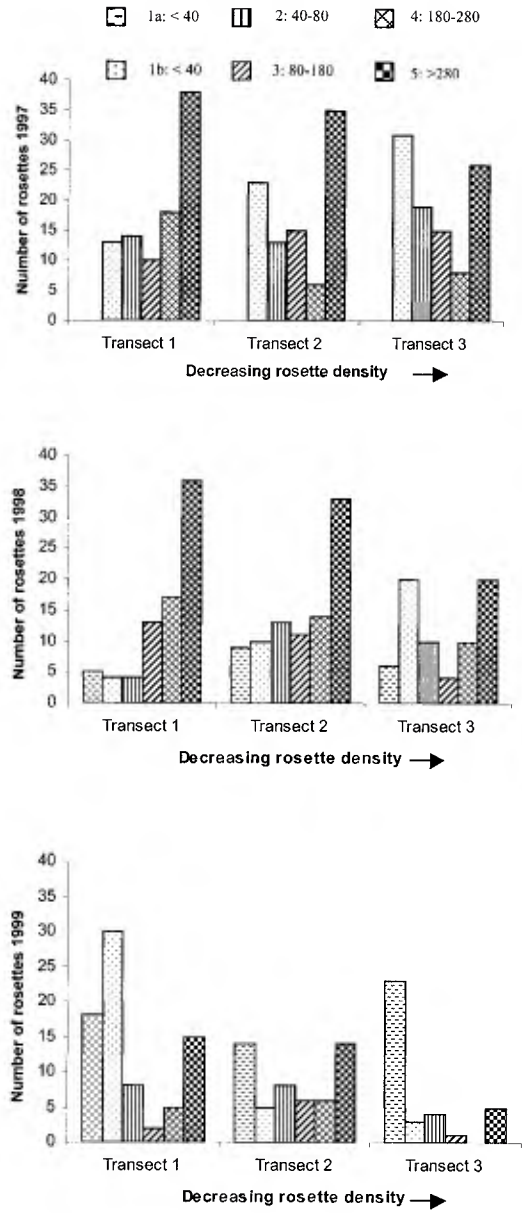


FIGURE 1. Stage class structure of *Aechmea magdalenae* populations in transects of differing densities, 1997–1999. Legend represents stage classes based on rosette width (cm): (1a) <40 and produced from dead mother rosettes, (1b) <40 and produced from live mother rosettes, (2) 40–80, (3) 80–180, (4) 180–280, and (5) >280. For rosette densities in transects see Table 1.

transects and had the smallest proportion of large plants. By the next census (November 1999), all transects showed evidence of peccary predation for rosettes in stage classes 3 and 4. Transects 1 and 2,

TABLE 2. Comparisons of mortality rates for *A. magdalenae* rosettes on Barro Colorado Island between 1997–1998 and 1998–1999. Values are means of the three transects \pm 1 SD.

Stage class ¹	Mortality rates	
	1997–1998	1998–1999 ²
1	0.786 \pm 0.054	0.819 \pm 0.005**
2	0.665 \pm 0.064	0.797 \pm 0.179
3	0.476 \pm 0.237	0.858 \pm 0.137*
4	0.006 \pm 0.006	0.624 \pm 0.087**
5	0.009 \pm 0.008	0.616 \pm 0.236*

¹ Stage classes represent rosette width (cm): (1) <40, (2) 40–80, (3) 80–180, (4) 180–280, and (5) >280.

² * $P < 0.05$, ** $P < 0.01$.

however, showed much lower levels of herbivory in stage class 5 than did Transect 3.

RATES AND PATTERNS OF RECRUITMENT.—Recruitment in *A. magdalenae* transects occurred in three ways: through vegetative propagation by rhizomes attached to living mother rosettes, through vegetative propagation by meristematic pieces of the underground stem of dead (eaten) rosettes, and by sexual reproduction. Rates of recruitment varied over the study period and among transects (Fig. 3).

The proportion of rosettes that were capable of vegetative propagation and that produced ramets surviving after one year dropped from 44 to 20 percent over the study period. Although the proportion of new ramets produced by living mother rosettes was lower in transect 1 than in the other two transects during the first year, the reverse was true during the second year. That is, in the second year, rosettes in transect 1 produced more ramets than those in transects 2 and 3. This was because the proportion of living rosettes that produced ramets surviving after one year increased over time in transect 1 but decreased from 1998 to 1999 in transects 2 and 3. Due to the variation in trends among transects, overall rates of vegetative propagation from live mother rosettes did not differ significantly between years ($df_{1, 2}$, $F = 2.36$, $P = 0.264$).

Rates of recruitment due to vegetative propagation from meristematic pieces of dead rosettes showed a different trend (Fig. 3). In the first census, no dead rosettes were observed and therefore no ramets emerging from pieces of dead rosettes were recorded. As a result of herbivory over the next two years, the proportion of dead rosettes steadily increased and the proportion of ramets

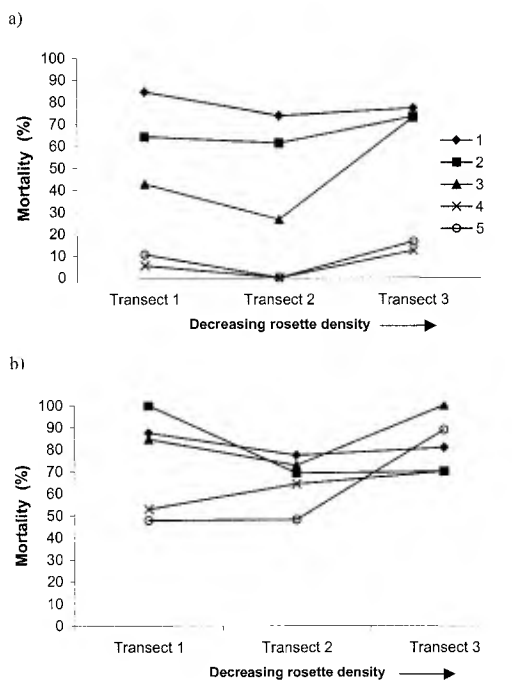
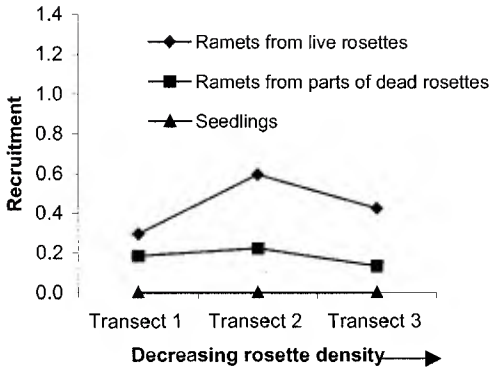


FIGURE 2. Per stage class mortality rates of *Aechmea magdalenae* rosettes in transects of differing densities, (a) November 1997–November 1998 and (b) November 1998–November 1999 on BCI. Legend represents stage classes based on rosette width (cm): (1) <40, (2) 40–80, (3) 80–180, (4) 180–280, and (5) >280. For rosette densities in transects see Table 1.

produced per dead rosette rose from 18 to 44 percent. After the first year, the proportion of dead rosettes producing ramets ranged from ca 13 to 18 percent and was similar among transects. After the second year, the proportion of dead rosettes producing ramets increased in transects 2 and 3, but particularly so in transect 1. Overall vegetative propagation from dead rosettes showed a tendency to increase over the two years ($df_{1, 2}$, $F = 9.55$, $P = 0.09$).

A total of 24 flowering rosettes was found in the transects during 1997 and 1 new flowering rosette appeared in 1998. Flowering rosettes took approximately one year to produce mature fruits and some seedlings were observed to be germinating on the mature fruit before they fell to the ground. No new seedlings were found in any of the transects during the first two censuses. In the third census (after the second year of the study), however, 0.81 new seedling per flowering rosette was recorded. Nearly 90 percent of these were found in transect

a)



b)

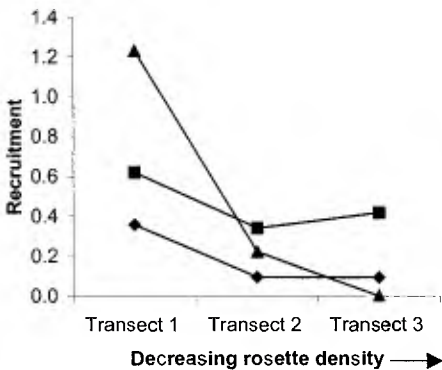


FIGURE 3. Rates of recruitment for *Aechmea magdalenae* in transects of differing densities, (a) 1997–1998 and (b) 1998–1999. Recruitment of ramets from live rosettes is the number of new ramets produced per total number of live rosettes capable of vegetative propagation. Recruitment from dead rosettes is the number of new ramets produced from dead rosettes per total number of dead rosettes. Recruitments of seedlings is the number of new seedlings produced per flowering rosette. For rosette densities in transects see Table 1.

1. The rest were found in transect 2, and in transect 3, no seedlings survived (Fig. 3).

EXCLOSURE EXPERIMENT.—For the enclosure experiment, seedlings that were growing inside enclosures and were therefore protected from trampling and herbivory by peccaries as well as other mammals, showed significantly higher rates of germination and survival after one year than did those growing outside the enclosures ($N = 360$, $df = 1$, $\chi^2 = 3.95$, $P = 0.046$). Of the 180 seeds planted inside a total of four enclosures, rates of germination and

survival after one year were 11, 18, 9, and 0 percent. Of the equal number of seeds planted outside the same enclosures, rates of germination and survival were 0, 11, 3, and 6 percent, respectively.

DISCUSSION

One of the consequences of the short duration of most plant demographic studies (Menges 2000) is that the effects of periodic environmental fluctuations are often overlooked. These fluctuations may, however, hold demographic and evolutionary implications. This study recorded the demographic behavior of *A. magdalenae* rosettes during an El Niño year with high levels of community-wide fruit production, and over the following two years with low levels of fruit production. This type of variation in community-wide fruit production and consequent change in food supply for frugivore populations has occurred periodically on BCI (Wright *et al.* 1999) and appears to affect demographic patterns of *A. magdalenae* in several ways.

RELATIONSHIPS BETWEEN COMMUNITY-WIDE FRUIT PRODUCTION AND MORTALITY OF *A. MAGDALENAE* ROSETTES.—The increasing rates of herbivory and mortality in the *A. magdalenae* population showed a close correspondence to the decreasing rates of community-wide fruit production associated with the 1997 ENSO (Wright *et al.*, pers. comm.). No herbivory was observed for the 1997 El Niño year, when fruit production was at its highest recorded level on BCI since 1987. As fruit production plummeted during the La Niña conditions of 1998, frugivores began to consume small rosettes and mortality rates in these stage classes rose. When fruit production remained well below average levels in 1999, high levels of herbivory were observed for rosettes of all sizes and the *A. magdalenae* population was reduced to almost half of its original size.

The elevated levels of mortality and herbivory in *A. magdalenae* populations associated with this ENSO event are striking because they contrast starkly with the low rates of mortality that have been reported for this species on BCI (Villegas 2001) and elsewhere (Ticktin 2000) and illustrate the importance of documenting the behavior of plants during environmental fluctuations. For example, Villegas found that mortality rates of large *A. magdalenae* rosettes from 1991 to 1993 on BCI were under 15 percent (Villegas 2001). These rates are consistent with those found during the first year of this study (when there was no herbivory), and are more than four times lower than those found

during the second year (when there was herbivory). Although Villegas recorded the dynamics of *A. magdalenae* populations during the 1992 El Niño event, her monitoring stopped just short of the ENSO-related famine that occurred from September to December of 1993 (Wright *et al.* 1999). Therefore, her data did not include the time period when *A. magdalenae* mortality rates would have been expected to be very high.

In general, *A. magdalenae* has been observed to suffer very little herbivory (Brokaw 1983) and the only published report of herbivory for this species is from late 1959, when coatis were observed digging up and eating the succulent stems of small *A. magdalenae* rosettes (Kaufman 1962). This period, however, is thought to have coincided with a frugivore famine associated with an ENSO event (Wright *et al.* 1999). While I did not observe any coati in the *A. magdalenae* population over the study period, it is possible that coati and/or other mammals may have also been responsible for herbivory damage.

The shift in diet of BCI peccaries to include *A. magdalenae* is consistent with peccary diet data from other locations. Peccaries living in seasonal rain forest habitats have been reported to change their diets to consume less fruits and more fibrous foods during seasons of fruit scarcity (Bodmer 1990, McCoy and Vaughan 1990). Similarly, peccaries living in more xeric biomes feed on less fruits and more roots, tubers, and leaves and succulent plant parts than rain forest peccaries (McCoy & Vaughan 1990, Olmos 1993, Martínez-Romero & Mandujano 1995, Barreto *et al.* 1997).

PECCARY FAMINE AND SELECTION PRESSURES IN *A. MAGDALENAE*.—The patterns of reproduction, survival, and mortality found in this study shed light on selective pressures faced by *A. magdalenae* populations in times of low community-wide fruit production and that are not apparent during most years. In particular, the finding that under high levels of herbivory, rosette mortality rates decrease with increasing population density suggests that there may be selection pressure for *A. magdalenae*'s dense growth habit. Under conditions of no herbivory, rates of vegetative propagation in *A. magdalenae* populations have been shown to be negatively density-dependent (Ticktin *et al.* 2003). This is due to high mortality of newly produced, highly shaded ramets. The low rates of vegetative propagation in the dense transect 1 during the first year of the study compared to the other transects appear to support this finding, since in this time period

there was no herbivory observed. In contrast, during the second year when herbivory was high, transect 1 had much higher rates of vegetative propagation and of seedling germination and survival than did the other less dense transects.

Similarly, transect 1 suffered the lowest overall mortality rates of rosettes since peccaries first ate the outer, most accessible rosettes of the other transects. The significantly higher rates of survival for seedlings inside exclosures also indicate that trampling by peccaries or herbivory by other mammals may increase mortality. Because *A. magdalenae* rosettes grow so densely, trampling is most likely to occur only in the outer edges of populations and in the least dense portions where peccaries can move between the very spiny leaves of the large rosettes.

By the end of 1999, some smaller and less dense *A. magdalenae* populations on other parts of BCI had completely disappeared as a result of herbivory (pers. obs.) Therefore, although herbivory or trampling has not been reported in any other study of this species, it is plausible that *A. magdalenae*'s dense growth habit may have evolved in part to prevent rosettes from trampling and herbivory during infrequent, but recurring, ENSO-related periods of fruit scarcity. In the past, herbivory may also have been carried out by the white-lipped peccary (*Tayassu albirsotris*), now extinct on BCI.

IMPLICATIONS FOR POPULATION REGULATION AND SEEDLING DISPERSAL.—By altering levels of community-wide fruit production and therefore affecting food supplies for frugivores, periodic El Niño events that are followed by years with low fruit production may play a role in regulating *A. magdalenae* populations. *Aechmea magdalenae* is capable of forming extensive colonies but the factors that limit population expansion have been largely unknown (Brokaw 1983). The 45 percent reduction in population size and the great decrease in the number of large rosettes capable of vegetative and sexual reproduction found in this study can be expected to have an effect on *A. magdalenae* population dynamics. Research on *A. magdalenae* population dynamics has shown that the largest stage classes contribute most to population growth, so that increases in their mortality rates have the greatest negative effects on population growth (Ticktin 2000, Villegas 2001). Therefore, periodic decreases associated with collared peccary famine may help keep *A. magdalenae* populations in check.

Wright *et al.* (1999) reported on the relationship between El Niño events with high commu-

nity-wide fruit production followed by mild dry seasons and low fruit production and fruit scarcity for frugivores. In this case, an El Niño event was followed by two years with low levels of fruit production. Had the second year (1999) not had low levels of fruit production, only rosettes in the smaller stage classes may have been eaten by peccaries. Although this pattern of mortality would have a lesser negative effect on population growth, it would still be expected to decrease population size (Ticktin *et al.* 2002). It is important to note here that although there were important increases in the number of new ramets produced by meristems of dead rosettes, these tend to have extremely low rates of growth and survival (Ticktin *et al.* 2003) and therefore would have little if any effect on population growth rates.

The environmental fluctuations associated with ENSO events that trigger changes in fruit availability for frugivores may also favor enhanced establishment and dispersal of *A. magdalenae* seedlings. Flowering of *A. magdalenae* appears to coincide with El Niño events (Villegas 2001; Ticktin, pers. obs.) and rosettes take at least one year to produce fruits. Thus, fruit production of *A. magdalenae* coincides with the low community-wide fruit production that often follows an El Niño year (Wright *et al.* 1999). This may make fruits particularly appealing to hungry frugivores such as peccaries, which can disperse small seeds (Barreto *et al.* 1997). Moreover, during 1998, herbivory of the small rosettes opened up new spaces within *A. magdalenae* populations. This appears to have permitted enhanced seedling survival, since seedlings that sprout up within existing populations are typically overshadowed by surrounding rosettes and usually die (Ticktin 2000). Indeed, although seedlings have rarely been observed in nature (Brokaw 1983, Ticktin 2000, Villegas 2001), *A. magdalenae* populations on BCI are genetically diverse (Murawski & Hamrick 1990). Enhanced sexual reproduction of *A. magdalenae* in El Niño years may be favorable for recruitment and dispersal of seedlings, and therefore may be critical for species survival when large portions of existing populations are destroyed by herbivory.

ENSO events followed by mild dry seasons occurred at differing intervals, five times over a 49 year period on BCI, and each time this sequence of events appears to have provoked fruit scarcity for frugivore populations (Wright *et al.* 1999). The intervals between these events ranged from 4

to 27 years. It is possible that the frequency at which ENSO events that stimulate enhanced levels of fruit community-wide fruit production are followed by years with low levels of fruit production may regulate *A. magdalenae* dynamics on both a population and metapopulation scale. The negative density-dependence exhibited by *A. magdalenae* rosettes and the enhanced survival of seedlings within populations after episodes of herbivory, suggest that individual populations probably undergo cycles of decrease due to herbivory followed by rapid growth during regeneration. The frequency at which frugivore populations face fruit scarcities—and search for alternate sources of food supplies—could therefore shape these cycles of growth and regeneration. Similarly, the fact that some small, less dense *A. magdalenae* populations disappeared as a result of herbivory also suggests that the probability of successful establishment of new populations may depend on the intervals between this sequence of climatic events. That is, if the pattern of ENSO events followed by mild dry seasons or simply low levels of fruit production were to occur more frequently, newly established populations might not have time to reach the density needed to protect them from total destruction by herbivory.

This short, three-year study offers a glimpse into some of the ways in which demographic patterns in one plant species may be influenced by climatic patterns, specifically El Niño events that stimulate community-wide fruit production followed by years with low levels of fruit production. Given that this type of environmental fluctuation has occurred periodically over the past century on BCI and appears to be associated with fruit scarcity for frugivore and granivore populations, it seems likely that it may also affect demographic and evolutionary patterns of other species that serve as famine foods or that interact in other ways with frugivores or granivores. Clearly, however, long-term monitoring will be necessary to better assess the implications of these environmental fluctuations for *A. magdalenae* and other species.

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