03058
2

UNIVERSIDAD NACIONAL AUTONOMA DE MEXICO

Unidad Académica de los Ciclos Profesional y
de Posgrado del C. C. H.

INSTITUTO DE ECOLOGIA

DISPERSIÓN BIÓTICA DE SEMILLAS DE *Neobuxbaumia tetetzo* (Coulter) Backeberg EN EL VALLE DE TEHUACÁN, PUEBLA

TESIS

QUE PARA OBTENER EL GRADO DE:

Doctor en Ecología

PRESENTA:

Héctor Octavio Godínez Alvarez

México, D. F.

Marzo 2000

275699

AGRADECIMIENTOS

Buena parte de mi formación académica se la debo al Dr. Alfonso Valiente Banuet, a quien conozco desde hace aproximadamente 10 años. A lo largo de todo este tiempo, la convivencia con el Vali ha contribuido a moldear la forma en la que percibo la ciencia y cómo debe de hacerse. Gracias a él, aprendí que la "historia natural" junto con una buena revisión y lectura de los trabajos científicos son fundamentales para desarrollar cualquier proyecto de investigación. Asimismo, aprendí que además de la academia es necesario desarrollar otras habilidades como establecer contactos con otras personas, hablar y escribir en inglés, trabajar en equipo y manejar la camioneta, entre muchas otras cosas más. Sin embargo, debo admitir que no todo fue color de rosa ya que, como buena relación que se establece entre dos *Homo sapiens* (?), hubo ocasiones en las que tuvimos diferencias de opinión y discusiones respecto de ciertos aspectos académicos y logísticos. Al final, debo reconocer que todas estas experiencias han sido de gran utilidad para mí, por lo que quiero agradecerle, de manera especial, su amistad y el haber fungido como mi asesor.

El comité tutorial que se encargó del seguimiento de la tesis a lo largo de todos los semestres que duró mi estancia en el posgrado estuvo integrado por Miguel Martínez Ramos, Rodrigo Medellín y Mario González Espinosa. A todos ellos les agradezco sus comentarios y sugerencias durante la realización del proyecto. Asimismo, quiero agradecer a Ma. del Coro Arizmendi, Miguel Verdú y Pascual Soriano con quienes tuve la oportunidad de discutir al inicio diversos aspectos metodológicos que fueron de gran ayuda para la elaboración del proyecto. La revisión final de la tesis estuvo a cargo del jurado integrado por María del Coro Arizmendi, Teresa Valverde, Miguel Martínez Ramos, Héctor Arita, Alejandro Casas, Alfonso Valiente Banuet y Francisco Molina. Todos sus comentarios ayudaron a mejorar la presentación final de la tesis y, en particular, a mejorar el manuscrito del último capítulo de la tesis.

El trabajo de campo necesario para cumplir con la tesis no hubiera sido posible sin la participación de varios amigos que, con flojera o sin ella, me ayudaron desinteresadamente en distintas etapas del proyecto: Adolfo Vital, Verónica Alvarado, Alberto Rojas, Oscar Osorio, Ariel Alcántara, Rocío José Jacinto, Rodolfo Reséndiz, José Antonio Soriano y Leticia Ríos. A todos ellos les doy las gracias. Asimismo quisiera agradecer a mis amigos Ariel Alcántara y Alberto Rojas con quienes siempre he discutido diversos temas "ecológicos", incluyendo por supuesto todos aquellos relacionados con nuestras tesis. Durante todos estos largos años que he permanecido en el posgrado he tenido la oportunidad de compartir la mesa del laboratorio, a la hora del desayuno y la comida, con mis compañeros y amigos Olga, Fofis, La Joseja, La Chana, Noé, Verónica, Oscar, Jorge, Lugui, Pablo, El Tío, Raymundo, Amelia, Carlos y Javier "El mini-McAuliffe". A todos ellos quiero darles las gracias por proporcionar "el material" necesario para que pasáramos ratos muy agradables burlándonos de nosotros mismos, del jefe y, por supuesto, de los personajes de otros laboratorios del instituto.

Obviamente, estos agradecimientos no estarían completos si no mencionara el apoyo económico recibido por parte de diversas instituciones tales como PADEP, FMCN, CONACyT y DGAPA. De la misma manera, debo agradecer a todo el personal de la "Panchita" por cocinar mis alimentos, por los partidos de basquetbol en los que fui bautizado como "Don Héctor" y por invitarme a fiestas infantiles para hacer así más llevadera mi estancia en Zapotitlán. Gracias a Rosa y a su mamá por prestarme los pájaros que me hacían falta para los ensayos de fisiología digestiva.

Finalmente, debo mencionar que el esfuerzo realizado a lo largo de todos estos años para obtener el doctorado no hubiera sido posible sin la ayuda de mi familia. Gracias a mi papá, por todo su respaldo y por su visión para insistirme en que estudiara inglés porque después me iba a servir de mucho. A mi mamá debo agradecerle también su apoyo, pero sobretodo, su ejemplo para demostrarme que echándole ganas todo lo que uno se proponga se puede lograr. A mi hermana y a Toño gracias por esos "vales" que me permitieron desahogar algunas de mis deudas. Gracias también por su comprensión y respeto para todas las cosas que hago. La Chanita, como la llaman ahora, se ha encargado de hacerme pasar ratos muy agradables y chistosos con todas las payasadas que se le ocurren. Gracias por todos los momentos que hemos compartido. Sin duda alguna, el apoyo de mi familia fue fundamental para poder obtener el grado.

CONTENIDO

Resumen

Introducción

Biotic interactions and the population dynamics of the long-lived columnar cactus *Neobuxbaumia tetetzo* in the Tehuacán Valley, Mexico

Germination and early seedling growth of Tehuacan Valley cacti species: the role of seed ingestion by dispersers on seedling growth

Fruit-feeding behavior of *Leptonycteris curasoae* and *Choeronycteris mexicana* in flight-cage experiments: consequences for dispersal of columnar cactus seeds

The role of seed dispersers in the population dynamics of the columnar cactus *Neobuxbaumia tetetzo*

Discusión

RESUMEN

Estudios recientes en zonas áridas y semiáridas han mostrado que las interacciones bióticas son comunes a lo largo del ciclo de vida de las especies, por lo que su análisis es fundamental para comprender la dinámica poblacional y comunitaria. El establecimiento de nuevos individuos es la etapa más crítica del ciclo de vida de las plantas y en ella ocurren diferentes interacciones como la dispersión, el comensalismo y la depredación. De todas estas interacciones, la dispersión de semillas por animales es la que ha sido menos estudiada en la ecología de los ambientes desérticos. Sin embargo, el estudio de esta interacción es necesario dado que representa un proceso que permitiría comprender el transporte de las semillas a sitios seguros ubicados debajo de plantas perennes, en donde existen condiciones adecuadas para la germinación y el establecimiento de plántulas. De esta forma, la dispersión hacia estos sitios incrementaría la probabilidad de sobrevivencia de semillas y plántulas, afectando considerablemente la dinámica poblacional de las plantas.

La cactácea columnar *Neobuxbaumia tetetzo* se distribuye en la región semiárida del Valle de Tehuacán-Cuicatlán, en el estado de Puebla. Esta cactácea crece asociada a plantas perennes debido a que la germinación y el establecimiento ocurren debajo de árboles y arbustos que disminuyen la radiación solar directa y la temperatura. Los frutos de esta planta son consumidos por diversos grupos de animales frugívoros tales como aves y murciélagos. Sin embargo, hasta antes del presente estudio, se desconocía cómo era el proceso de dispersión de las semillas y su relación con el reclutamiento de los nuevos individuos.

En este trabajo se presentan los resultados de una investigación cuyos principales objetivos fueron estudiar la dispersión de las semillas y determinar su efecto sobre la dinámica poblacional de *Neobuxbaumia tetetzo*. Los resultados obtenidos se presentan en cuatro artículos que actualmente se encuentran en distintas etapas del proceso de publicación. En el primer artículo, titulado 'Biotic interactions and the population dynamics of the long-lived columnar cactus *Neobuxbaumia tetetzo* in the Tehuacán Valley, Mexico' se presenta el estudio demográfico de *N. tetetzo* utilizando modelos matriciales y considerando que las semillas son dispersadas de manera aleatoria en el ambiente. Los resultados muestran que el estudio de las interacciones bióticas que una planta establece a lo largo de su ciclo de vida es importante para comprender su dinámica poblacional. En particular, el estudio de la dispersión es necesario dado que la sobrevivencia de las primeras etapas del ciclo de vida depende del transporte de las semillas a sitios específicos localizados debajo de árboles y arbustos. Este trabajo fue publicado en la revista **Canadian Journal of Botany** en 1999.

El segundo artículo de la tesis, 'Germination and early seedling growth of Tehuacán Valley cacti species: the role of soils and seed ingestion by dispersers on seedling growth', trata diversos aspectos de la germinación de las semillas de diferentes especies de cactáceas, entre las que se encuentra *N. tetetzo*. En este trabajo se aplicaron experimentalmente diversos tratamientos a las semillas y se evaluó su efecto sobre la germinación. Uno de estos tratamientos consistió precisamente en simular el efecto del paso por el tracto digestivo sobre las semillas como si éstas hubieran sido consumidas por algún animal. Los resultados mostraron que las semillas de las cactáceas resisten una amplia variedad de tratamientos, inclusive la inmersión en ácido clorhídrico, debido a que no afectan la germinación. Este trabajo fue

publicado en la revista **Journal of Arid Environments** en 1998.

En el tercer artículo, titulado 'Fruit-feeding behavior of *Leptonycteris curasoae* and *Choeronycteris mexicana* in flight cage experiments: consequences for dispersal of columnar cactus seeds', se presenta un estudio de los patrones de forrajeo y comportamiento de dos especies de murciélagos glosofáginos. Estas dos especies de murciélagos son los principales consumidores nocturnos de los frutos de *N. tetetzo*. En este trabajo, además de reportar cómo es su comportamiento durante el consumo de los frutos, se discuten las implicaciones que éste tiene para la dispersión de las semillas y la sobrevivencia de las plántulas. Este trabajo fue aceptado para su publicación en la revista **Biotropica** y actualmente se encuentra en prensa.

Finalmente en el cuarto artículo, 'The role of seed dispersers in the population dynamics of the columnar cactus *Neobuxbaumia tetetzo*', se muestra evidencia que apoya la hipótesis de la dispersión dirigida de las semillas de esta cactácea a los sitios seguros para su germinación y sobrevivencia. Para esto se empleó un índice que consideró la cantidad y la calidad de la dispersión realizada por diversas especies de consumidores, el cual permitió determinar cuál es la especie de frugívoro que 'brinda los mejores servicios' para *N. tetetzo*. Con base en este índice, y considerando los modelos matriciales reportados en el primer trabajo, se modificaron las entradas de la matriz correspondientes a la fecundidad para incorporar el efecto de la dispersión en la dinámica poblacional. Los resultados muestran que el impacto de los dispersores sobre la tasa finita de crecimiento poblacional varían según la especie que se trate. Este trabajo será enviado para su evaluación a la revista **Ecology**.

Con base en la información obtenida en los trabajos anteriores, al final de la tesis, se discuten las implicaciones ecológicas y evolutivas de la dispersión de semillas por animales para las cactáceas columnares y para los ambientes desérticos.

ABSTRACT

Recent studies in arid and semiarid zones have shown that biotic interactions are common in the life cycle of plants; therefore their study is essential to understand the dynamics of populations and communities. The establishment of new individuals is considered the most critical phase of the life cycle of plants in which several biotic interactions occur such as seed dispersal, facilitation and predation. Seed dispersal by animals is the less studied interaction in the ecology of deserts. However studies on this interaction are necessary because they will provide information on the transport of seeds to safes sites beneath trees and shrubs where seed germination and seedling establishment occur. Moreover seed dispersal could enhance the survival probability of seeds and seedlings, affecting the population dynamics of plants.

The columnar cactus *Neobuxbaumia tetetzo* inhabits the Tehuacán Valley, in the state of Puebla. This columnar cactus grows associated to trees and shrubs, because seed germination and seedling establishment occur in safe sites located under the canopy of these plants, where radiation and temperature decrease. Its fruits are consumed by a wide array of frugivores, including some species of birds and bats. Despite this fact, it is unknown how do seeds are dispersed and its effects on the recruitment of new individuals to the populations.

This work presents the results of an investigation whose main objectives were to analyze the seed dispersal of *Neobuxbaumia tetetzo* and to determine their effects on the population dynamics of this columnar cactus. The results are summarized in four papers that are or will be published in different journals. The first paper, 'Biotic interactions and the population dynamics of the long-lived columnar cactus *Neobuxbaumia tetetzo* in the Tehuacán Valley, Mexico', analyzes the demography of *N. tetetzo* using a matrix model approach and considering that seeds are dispersed randomly in the environment. The results indicate that the study of biotic interactions is essential to understand the population dynamics of columnar cacti. Particularly, the analysis of seed dispersal is important since the survival of the first life-cycle stages depends on the dispersal of seeds to safe sites under trees and shrubs. This paper was published in the **Canadian Journal of Botany** 77:203-208 (1999).

The second paper, 'Germination and early seedling growth of Tehuacán Valley cacti species: the role of soils and seed ingestion by dispersers on seedling growth', analyzes the seed germination of different species of cactus, including *N. tetetzo*. Different experimental treatments were used and their effects on germination tested; one of these treatments simulated the passage of seeds through the digestive tract. The results indicate that cactus seeds could germinate in a wide variety of conditions. This paper was published in the **Journal of Arid Environments** 39:21-31 (1998).

The third paper, 'Fruit-feeding behavior of *Leptonycteris curasoae* and *Choeronycteris mexicana* in flight cage experiments: consequences for dispersal of columnar cactus seeds', presents the foraging patterns and the fruit-feeding behavior of two species of phyllostomid bats. These bats are among the main consumers of the *N. tetetzo* fruits. This work discusses the implications of the foraging behavior of bats on seed dispersal and seedling survival of cactus. This paper has been accepted for publication in **Biotropica**.

Finally, the paper, 'The role of seed dispersers in the population dynamics of the

columnar cactus *Neobuxbaumia tetetzo*', shows evidence that supports the hypothesis that *N. tetetzo* seeds are dispersed to safe sites in which seed germination and seedling establishment occurs. The seed dispersal effectiveness of different species of frugivores was determined considering the quantity and quality of dispersal. Considering the seed dispersal effectiveness of each frugivore and the matrix model reported in the first paper, the fecundity values of the matrix were modified to incorporate the effect of seed dispersal on the population dynamics. The results indicate that the effect of frugivores on the population finite rate of increase varies according to species. This paper will be submitted to **Ecology.**

Considering the information obtained in the previous papers, the ecological and evolutionary consequences of seed dispersal for columnar cacti and desert communities are discussed.

INTRODUCCION

Las interacciones bióticas que se establecen entre las diferentes especies que conforman una comunidad pueden afectar la ecología y la evolución de los interactuantes (Howe & Smallwood 1982, Howe 1986). La cantidad de trabajos en la literatura sobre el tema, aparte de ser numerosa, hace énfasis principalmente en el hecho de que las interacciones bióticas generan procesos de selección natural que determinan las adaptaciones de los organismos, promoviendo así los cambios evolutivos (Abrahamson 1989). Se ha demostrado que la existencia de diversas interacciones en las comunidades favorece el establecimiento de complejas redes tróficas las cuales afectan la dinámica de las poblaciones y la estructura de las comunidades (Levins & Lewontin 1985, Polis 1991).

No obstante su importancia, el estudio de las interacciones bióticas en zonas áridas ha ocupado un lugar secundario, aún cuando su presencia ya había sido reportada desde principios de siglo en diferentes trabajos (Shreve 1929, 1931, 1942). Esta situación se debe a que tradicionalmente los ecosistemas desérticos han sido considerados como sistemas en los cuáles tanto los procesos poblacionales como el mantenimiento de la diversidad están determinados por la dinámica y cantidad del agua (Noy-Meir 1973), por lo que únicamente los estudios con enfoques autoecológicos han ocupado un papel preponderante en los estudios ecológicos en estas regiones (Noy-Meir 1980).

Sin embargo, estudios realizados en diferentes zonas áridas del mundo indican que las interacciones bióticas en estos sistemas son comunes durante las distintas etapas del ciclo de vida de las especies (Steenbergh & Lowe 1969, Fowler 1986, Hutto *et al.* 1986, Valiente-Banuet & Ezcurra 1991, Flores-Martínez *et al.* 1994, Suzán *et al.* 1996, Valiente-Banuet *et al.* 1997a, b) y que su estudio es fundamental para comprender la dinámica poblacional y comunitaria (McAuliffe 1988, Polis 1991, Valiente Banuet 1991). Asimismo, el estudio reciente de las interacciones bióticas ha mostrado que éstas, particularmente las interacciones de índole positivo, favorecen la coexistencia de las especies en ambientes estresantes tales como desiertos y pastizales alpinos (Callaway & Walker 1997, Hacker & Gaines 1997, Holmgren *et al.* 1997). Así, interacciones como la polinización y la facilitación son esenciales para la permanencia de las especies en estos ambientes (Valiente Banuet 1991, Valiente-Banuet *et al.* 1997a, b).

De todas las etapas del ciclo de vida, el establecimiento de nuevos individuos en las poblaciones de plantas es la más crítica (Harper 1977). En los desiertos esta etapa se caracteriza por ocurrir bajo condiciones de impredecibilidad climática, altos niveles de radiación (Noy-Meir 1973, Valiente Banuet 1991) y depredación post-dispersión (Valiente-Banuet & Ezcurra 1991). El establecimiento exitoso de nuevos individuos de un gran número de especies ocurre únicamente bajo la copa de árboles y arbustos perennes denominados plantas nodriza (Valiente Banuet 1991). En la actualidad se ha llegado a reconocer que, en ocasiones, hasta el 50% de las especies de una comunidad presentan este patrón de establecimiento asociado a plantas nodriza (McAuliffe 1988, Valiente Banuet 1991), por lo que los aspectos microambientales son considerados como factores importantes en estos ambientes (McAuliffe 1988, Valiente-Banuet *et al.* 1991). Es precisamente durante el establecimiento cuando ocurren diferentes interacciones bióticas como la dispersión, el comensalismo y la depredación, sin embargo la importancia relativa de cada una de estas interacciones sobre el proceso de establecimiento no ha sido aun determinada de manera integral en ningún sistema desértico (Valiente Banuet 1991). El estudio detallado de las interacciones permitiría no sólo determinar su papel en la explicación del patrón asociado que presentan muchas especies (Hutto *et al.* 1986) sino que también permitiría comprender su efecto sobre la dinámica poblacional (McAuliffe 1988).

De todas las interacciones presentes durante el establecimiento, la dispersión de semillas por animales es la que ha sido menos estudiada en la ecología de las zonas áridas (Jordano 1992). En estos ambientes se considera que la producción de frutos carnosos es muy baja debido a la escasa precipitación y humedad, por lo que la endozoocoria es poco importante o inexistente (Jordano 1992) o bien, que las condiciones ambientales extremas han determinado la ausencia de características que favorezcan la dispersión (*i. e.* atelocoria; Ellner & Shmida 1981). Sin embargo, la dispersión por animales podría ser un mecanismo de gran relevancia para la explicación de los procesos señalados anteriormente. En este sentido, diversos trabajos (Steenbergh & Lowe 1977, Hutto *et al.* 1986, McAuliffe 1988, Olin *et al.* 1989, Valiente-Banuet *et al.* 1996) han señalado que la dispersión por animales es un proceso que permitiría el transporte de las semillas a sitios seguros localizados por debajo de plantas nodrizas, en donde existen condiciones adecuadas para la germinación, y además incrementaría la probabilidad de sobrevivencia de semillas y plántulas. Como consecuencia, la dispersión de las semillas por animales tendría un efecto considerable sobre la dinámica poblacional de las especies.

Los estudios sobre la ecología de la dispersión realizados durante los últimos años en zonas desérticas (tabla 1) han estado enfocados al análisis de solamente alguna de las diferentes etapas que conforman el proceso de establecimiento como la dispersión de las semillas, los patrones de germinación o bien, la sobrevivencia de las plántulas. Así, la determinación de las características de los frutos y la identificación de los agentes dispersores, incluyendo sus patrones de consumo espacial y temporal, han sido el objetivo principal de la mayoría de estos trabajos (Steenbergh & Lowe 1977, Davidson & Morton 1981, 1984, Silva 1988, Wendelken & Martin 1988, Reid 1989, León de la Luz & Cadena 1991, Soriano *et al.* 1991, Knoch *et al.* 1993, Silvius 1995). Otros estudios también han evaluado el efecto del consumo de los frutos sobre las semillas realizando pruebas de germinación con semillas ingeridas para cuantificar la velocidad y el porcentaje final de germinación (Steenbergh & Lowe 1977, Silva 1988, Olin *et al.* 1989, Reid 1989, León de la Luz & Cadena 1991, Knoch *et al.* 1993, Silvius 1995). Finalmente, otros trabajos han tenido como objetivo determinar la sobrevivencia de las plántulas en diferentes micrositios considerando las preferencias de hábitat de las diferentes especies de dispersores y depredadores de semillas (Vargas-Mendoza & González-Espinosa 1992). La información generada por estos trabajos es valiosa para comprender el efecto de los dispersores sobre el reclutamiento de nuevos individuos en las poblaciones, sin embargo, es necesario realizar un análisis detallado de la dispersión que integre las distintas etapas del proceso con el fin de determinar su efecto sobre la dinámica poblacional.

En este trabajo se presentan los resultados de una investigación cuyos principales objetivos fueron estudiar la dispersión de las semillas y determinar su efecto sobre la dinámica poblacional de *Neobuxbaumia tetetzo*, una cactácea columnar que se distribuye en la región semiárida del Valle de Tehuacán-Cuicatlán, en el estado de Puebla. Esta cactácea, que puede alcanzar hasta 8 m de altura y ocupar como especie dominante extensiones de hasta 400 km^2, crece asociada a plantas perennes debido a que la germinación de las semillas y el establecimiento de las plántulas ocurre debajo de plantas nodriza que disminuyen la radiación solar directa y la temperatura, facilitando así dichos procesos (Valiente-Banuet *et al.* 1991). Sus frutos son verdes, dehiscentes y se producen en el ápice de los tallos. Al abrir, exponen las semillas con sus funículos blanquecinos y azucarados, los cuales poseen un aroma y color muy similar al de las flores que son polinizadas por murciélagos (Valiente-Banuet *et al.* 1996). Todas estas características sugieren que los frutos presentan un síndrome de quiropterocoria (van der Pijl 1982), por lo que los murciélagos serían los principales dispersores de las semillas de esta especie. Durante la fructificación de *N. tetetzo*, diferentes especies de murciélagos son muy abundantes y consumen las semillas de una gran variedad de cactáceas columnares (Rojas-Martínez *et al.* in prep.). Además, diferentes especies de aves e insectos también se alimentan de los frutos de esas plantas (Valiente-Banuet *et al.* 1996).

Esta evidencia sugiere que los frutos de *N. tetetzo* podrían ser consumidos por diversos grupos de animales frugívoros. Sin embargo, hasta antes del presente estudio se desconocía cómo era el proceso de dispersión de estas semillas y su relación con el reclutamiento de los nuevos individuos. No se tenía información sobre la cantidad de semillas consumida por estos organismos y la calidad del tratamiento que le proporcionan a las semillas. Asimismo, se ignoraba si la dispersión disminuía el riesgo de depredación de las semillas, incrementando así su probabilidad de germinación y sobrevivencia.

Para responder a estas interrogantes se llevó a cabo un proyecto de investigación entre los años de 1996 y 1997. Los resultados obtenidos se presentan en cuatro artículos que fueron enviados a diferentes revistas y que actualmente se encuentran en distintas etapas del proceso de evaluación y publicación. En el primer trabajo, titulado 'Biotic interactions and the population dynamics of the long-lived columnar cactus *Neobuxbaumia tetetzo* in the Tehuacan Valley, Mexico' se presenta el estudio demográfico de *N. tetetzo* utilizando modelos matriciales y considerando que las semillas son dispersadas de manera aleatoria en el ambiente. Los resultados muestran que el estudio de las interacciones bióticas que una planta establece a lo largo de su ciclo de vida es importante para comprender su dinámica poblacional. En particular, el estudio de la dispersión es necesario dado que la sobrevivencia de las primeras etapas del ciclo de vida depende del transporte de las semillas a sitios específicos localizados debajo de árboles y arbustos. Este trabajo fue publicado en la revista **Canadian Journal of Botany** en 1999.

El segundo trabajo de la tesis, 'Germination and early seedling growth of Tehuacán Valley cacti species: the role of soils and seed ingestion by dispersers on seedling growth', trata diversos aspectos de la germinación de las semillas de diferentes especies de cactáceas, entre las que se encuentra *N. tetetzo*. En este trabajo se aplicaron experimentalmente diversos tratamientos a las semillas y se evaluó su efecto sobre la germinación. Uno de estos tratamientos consistió precisamente en simular el efecto del paso por el tracto digestivo sobre las semillas como si éstas hubieran sido consumidas por algún animal. Los resultados mostraron que las semillas de las cactáceas resisten una amplia variedad de tratamientos, inclusive la inmersión en ácido clorhídrico, debido a que no afectan la germinación. Este trabajo fue publicado en la revista **Journal of Arid Environments** en 1998.

En el tercer trabajo, titulado 'Fruit-feeding behavior of *Leptonycteris curasoae* and *Choeronycteris mexicana* in flight cage experiments: consequences for dispersal of columnar cactus seeds', se presenta un estudio de los patrones de forrajeo y comportamiento de dos especies de murciélagos glosofáginos. Estas dos especies de murciélagos son los principales consumidores nocturnos de los frutos de *N. tetetzo*. En este trabajo, además de reportar cómo es su comportamiento durante el consumo de los frutos, se discuten las implicaciones que éste tiene para la dispersión de las semillas y la sobrevivencia de las plántulas. Este trabajo fue aceptado para su publicación en la revista **Biotropica** y actualmente se encuentra en prensa.

Finalmente en el cuarto trabajo, 'The role of seed dispersers in the population dynamics of the columnar cactus *Neobuxbaumia tetetzo*', se muestra evidencia que apoya la hipótesis de la dispersión dirigida de las semillas de esta cactácea a los sitios seguros para su germinación y sobrevivencia. Para esto se empleó un índice que consideró la cantidad y la calidad de la dispersión realizada por diversas especies de consumidores, el cual permitió determinar cuál es la especie de frugívoro que 'brinda los mejores servicios' para *N. tetetzo*. Con base en este índice, y considerando los modelos matriciales reportados en el primer trabajo, se modificaron las entradas de la matriz correspondientes a la fecundidad para incorporar el efecto de la dispersión en la dinámica poblacional. Los resultados muestran que el impacto de los dispersores sobre la tasa finita de crecimiento poblacional varían según la especie que se trate. Este trabajo será enviado para su evaluación a la revista **Ecology**.

REFERENCIAS

Abrahamson, W.C. 1989. Plant-animal interactions: an overview. In: Abrahamson, W.C. (ed). *Plant-Animal Interactions*. McGraw-Hill Book Company.

Callaway, R. & Walker, L. R. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78(7):1958-1965.

Davidson, D. W. & Morton, S. R. 1981. Myrmecochory in some plants (*F. chenopodiaceae*) of the australian arid zone. *Oecologia (Berl)* 50:357-366.

Davidson, D. W. & Morton, S. R. 1984. Dispersal adaptations of some *Acacia* species in the australian arid zone. *Ecology* 65(4):1038-1051.

Ellner, S. & Shmida, A. 1981. Why are adaptations for long-range seed dispersal rare in desert plants?. *Oecologia (Berl)* 51:133-144.

Fleming, T. H. & Sosa, V. J. 1994. Effects of nectarivorous and frugivorous mammals on reproductive success of plants. *Journal of Mammalogy* 75(4):845-851.

Flores-Martinez, A., Ezcurra, E. & Sánchez-Colón, S. 1994. Effect of *Neobuxbaumia tetetzo* on growth and fecundity of its nurse plant *Mimosa luisana*. *Journal of Ecology* 82:325-330.

Fowler, N. 1986. The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecology and Systematics* 17:89-110.

Hacker, S. D. & Gaines, S. D. 1997. Some implications of direct positive interactions for community species diversity. *Ecology* 78(7):1990-2003.

Harper, J. L. 1977. *Population Biology of Plants.* Academic Press. New York.

Holmgren, M., Scheffer, M. & Huston, M. A. 1997. The interplay of facilitation and competition in plant communities. *Ecology* 78(7):1966-1975.

Howe, H. F. 1986. Seed dispersal by fruit-eating birds and mammals. In: Murray, D. R. (ed.). *Seed dispersal.* Academic Press. Australia.

Howe, H. F. & Smallwood, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13:201-228.

Hutto, R. L., McAuliffe, J. R. & Hogan, L. 1986. Distributional associates of the Saguaro (*Carnegiea gigantea*). *The Southwestern Naturalist* 31(4):469-476.

Jordano, P. 1992. Fruits and frugivory. In: Fenner, M. (ed.). *Seeds. The ecology of regeneration in plant communities*. Redwood Press. United Kingdom.

Knoch, T. R., Faeth, S. H. & Arnott, D. L. 1993. Endophytic fungi alter foraging and dispersal by desert seed-harvesting ants. *Oecologia* 95:470-473.

León de la Luz, J. L. & Cadena, R. D. 1991. Evaluación de la reproducción por semilla de la pitaya agria (*Stenocereus gummosus*) en Baja California Sur, México. *Acta Botánica Mexicana* 14:75-87.

Levins R. & Lewontin, R. 1985. *The Dialectical Biologist*. Harvard University Press, Cambridge.

McAuliffe, J. R. 1988. Markovian dynamics of simple and complex desert plant communities. *The American Naturalist* 131(4):459-490.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4:25-51.

Noy-Meir, I. 1980. Structure and function of desert ecosystems. *Israel Journal of Botany* 28:1-19.

Olin, G., Alcorn, S. M. & Alcorn, J. M. 1989. Dispersal of viable saguaro seeds by white-winged doves (*Zenaida asiatica*). *The Southwestern Naturalist* 34:282-284.

Polis, G. A. 1991. Desert communities: An overview of patterns and processes. In: Polis, G. A. (ed.). *The ecology of desert communities*. The University of Arizona Press. Tucson, USA.

Reid, N. 1989. Dispersal of mistletoes by honeyeaters and flowerpeckers: components of seed dispersal quality. *Ecology* 70:137-145.

Rojas-Martínez, A., Godínez-Alvarez, H., Valiente-Banuet, A., Arizmendi, M. del C. & Soriano, A. in prep. Columnar cacti fruits: an important food resource for phyllostomid bats in the Tehuacán Valley, Mexico.

Shreve, F. 1929. Changes in desert vegetation. *Ecology* 10:364-373.

Shreve, F. 1931. Physical conditions in sun and shade. *Ecology* 12:96-104.

Shreve, F. 1942. The desert vegetation of North America. *Botanical Review* 8:195-246.

Silva, W. R. 1988. Ornitocoria em *Cereus peruvianus* (Cactaceae) na Serra do Japi, Estado de São Paulo. *Revista Brasileira de Biologia*. 48(2):381-389.

Silvius, K. M. 1995. Avian consumers of cardón fruits (*Stenocereus griseus*: Cactaceae) on Margarita Island, Venezuela. *Biotropica* 27(1):96-105.

Soriano, P. J., Sosa, M. & Rossell, O. 1991. Hábitos alimentarios de *Glossophaga longirostris* Miller (Chiroptera: Phyllostomidae) en una zona árida de los Andes venezolanos. *Revista de Biología Tropical* 39(2):263-268.

Steenbergh, W. H. & Lowe, C. H. 1969. Critical factors during the first years of life of the saguaro (*Cereus giganteus*) at the Saguaro National Monument, Arizona. *Ecology* 50(5):825-834.

Steenbergh, W. F. & Lowe, C. H. 1977. Ecology of the saguaro II. Reproduction, germination establishment, growth and survival of the young plant. *Nat. Park Serv. Sci. Monogr. Ser. No. 8. Washington, D. C.*

Suzán, H., Nabhan, G. & Patten, D. T. 1996. The importance of *Olneya tesota* as a nurse plant in the Sonoran Desert. *Journal of Vegetation Science* 7:635-644.

Valiente Banuet, A. 1991. Dinámica del establecimiento de cactáceas: Patrones generales y consecuencias de los procesos de facilitación por plantas nodriza en desiertos. *Tesis de Doctorado. Centro de Ecología, UNAM. México.*

Valiente-Banuet, A., Bolongaro-Crevenna, A., Briones, O., Ezcurra, E., Rosas, M., Núñez, H., Barnard, G. & Vázquez, E. 1991. Spatial relationships between cacti and nurse shrubs in a semi-arid environment in central Mexico. *Journal of Vegetation Science* 2:15-20.

Valiente-Banuet, A. & Ezcurra, E. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán Valley, Mexico. *Journal of Ecology* 79:961-971.

Valiente-Banuet, A., Arizmendi, M. del C., Rojas-Martínez, A. & Domínguez, L. 1996. Ecological relationships between columnar cacti and nectar-feeding bats in Mexico. *Journal of Tropical Ecology* 12:103-119.

Valiente-Banuet, A., Rojas-Martínez, A., Arizmendi, M. del C. & Dávila, P. 1997a. Pollination biology of two columnar cacti (*Neobuxbaumia mezcalaensis* and *Neobuxbaumia macrocephala*) in the Tehuacán Valley, central Mexico. *American Journal of Botany* 84(4):452-455.

Valiente-Banuet, A., Rojas-Martínez, A., Casas, A., Arizmendi, M. del C. & Dávila, P. 1997b. Pollination biology of two winter-blooming giant columnar cacti in the Tehuacán Valley, central Mexico. *Journal of Arid Environments* 37:331-341.

van der Pijl, L. 1982. *Principles of dispersal in higher plants.* Springer-Verlag. Berlin.

Vargas-Mendoza, M. C. & González-Espinosa, M. 1992. Habitat heterogeneity and seed dispersal of *Opuntia streptacantha* (Cactaceae) in nopaleras of central Mexico. *The Southwestern Naturalist* 37(4):379-385.

Wendelken, P. W. & Martin, R. F. 1988. Avian consumption of the fruit of the cacti *Stenocereus eichlamii* and *Pilosocereus maxonii* in Guatemala. *The American Midland Naturalist* 119(2):235-243.

Yan, Z. 1993. Seed dispersal of *Amyema preissii* and *Lysiana exocarpi* by mistletoebirds and spiny-cheeked honeyeaters. *Emu* 93:214-219.

Tabla 1. Trabajos encontrados en la literatura sobre dispersión biótica en diferentes zonas áridas y semiáridas. La revisión bibliográfica abarca desde el año de 1977 hasta 1995.

Planta (s)	**Dispersor (es)**	**Cita**
Carnegiea gigantea	Diferentes especies de insectos, aves y mamíferos	Steenbergh & Lowe 1977
Familia Chenopodiaceae	Hormigas	Davidson & Morton 1981
Acacia (20 spp.)	Aves y hormigas	Davidson & Morton 1984
Cereus peruvianus	*Thraupis sayaca* *Zonotrichia capensis* *Coryphosphingos cucullatus*	Silva 1988
Stenocereus eichlamii *Pilosocereus maxonii*	Aves (18 spp.)	Wendelken & Martin 1988
Carnegiea gigantea	*Zenaida asiatica*	Olin, Alcorn & Alcorn 1989
Amyema quandang	*Anathagenys rufogularis* *Dicaeum hirundinaceum*	Reid 1989
Stenocereus gummosus	Diferentes especies de insectos, reptiles, aves y mamíferos	León de la Luz & Cadena 1991
Stenocereus griseus *Subpilocereus repandus* *Pilosocereus tillianus*	*Glossophaga longirotris*	Soriano, Sosa & Rossell 1991
Opuntia streptacantha	Roedores y hormigas	Vargas-Mendoza & González-Espinosa 1992
Festuca arundinacea	*Pogonomyrmex rugosus* *P. occidentalis*	Knoch, Faeth & Arnott 1993
Amyema preissii *Lysiana exocarpi*	*Anathagenys rufogularis* *Dicaeum hirundinaceum*	Yan 1993
Diferentes especies de plantas	Diferentes especies de mamíferos	Fleming & Sosa 1994 (Artículo de revisión)
Stenocereus griseus	Aves (14 spp.)	Silvius 1995

Biotic interactions and the population dynamics of the long-lived columnar cactus *Neobuxbaumia tetetzo* in the Tehuacán Valley, Mexico

Héctor Godínez-Alvarez, Alfonso Valiente-Banuet, and Leopoldo Valiente Banuet

Abstract: The giant columnar cactus *Neobuxbaumia tetetzo* (Coulter) Backeberg is the dominant species of a vegetation type locally called "tetechera" that occupies ca. 400 km^2 in the Tehuacán Valley. As a way to analyse the role of biotic interactions on the population dynamics of this species, we conducted an elasticity analysis, using matrix models elaborated from field data, to determine the finite rate of increase and the critical stages of the life cycle that were related to the biotic interactions occurring during these stages. Although the estimated finite rate of increase did not differ from unity there were significant differences between the actual and predicted size distributions. Elasticity analysis showed that survivorship was the most important life-history parameter to the finite rate of increase. Because survivorship depends on the presence of nurse plants, our results emphasise the importance of positive interactions on the population dynamics of long-lived columnar cacti.

Key words: biotic interactions, Cactaceae, deserts, matrix models, population dynamics.

Résumé : Le cactus columnaire géant *Neobuxbaumia tetetzo* (Coulter) Backeberg est l'espèce dominante d'un type de végétation localement appelé « tetechera » qui occupe environ 400 km^2 dans la vallée de Tehuacán. De manière à analyser le rôle des interactions biotiques sur la dynamique des populations de cette espèce, les auteurs ont conduit une étude d'élasticité en utilisant des modèles matriciels construits à partir de données de terrain, et ceci de façon à déterminer le taux limite d'augmentation et les stades critiques du cycle vital qui sont reliés aux interactions biotiques survenant au cours de ces étapes. Bien que le taux limite estimé d'augmentation ne diffère pas de l'unité, il y a des différences significatives entre les distribution des grandeurs réelles et estimées. L'analyse d'élasticité montre que le comportement de survie est le paramètre le plus important du cycle vital pour le taux limite d'augmentation. Parce que la capacité de survie dépend de la présence de plantes compagnes, les résultats appuient l'importance des interactions positives sur la dynamique des populations des cactus columnaires à longue durée de vie.

Mots clés : interactions biotiques, Cactaceae, déserts, modèles matriciels, dynamique des populations.

[Traduit par la Rédaction]

Introduction

Recent studies on pollination, seed dispersal, establishment, predation, and competition conducted with columnar cacti in North America (McAuliffe 1984*a*; Valiente-Banuet et al. 1991*a*, 1991*b*, 1996, 1997*a*, 1997*b*), have shown that biotic interactions play an important role in the maintenance of populations in arid environments. These studies provide an important ecological context in which to determine the role of these interactions on the population dynamics of cacti. We propose that, to do this, it is necessary first to assess the critical phases of the life cycle of populations and then to verify the nature of the biotic interactions affecting those critical stages to determine their relative importance. Matrix models represent a useful tool that permits us to ascertain the relative contribution made by different life stages to the finite rate of increase (λ) and to determine in which stages of the life cycle other species might be playing an important role in population regulation (Caswell 1989).

Demographic studies in columnar cacti have proposed that germination and seedling establishment are the most critical phases of the life cycle (Steenbergh and Lowe 1969). Successful seedling establishment occurs only in safe microsites (sensu Harper 1977) located beneath the canopies of perennial plants (Shreve 1931; Turner et al. 1966; Steenbergh and Lowe 1969; Valiente-Banuet and Ezcurra 1991). At the same time, nurse plants may also provide protection against predators, hence increasing the probability of cactus-seedling survivorship (Niering et al. 1963; Turner et al. 1966; McAuliffe 1984*a*, 1986). Birds and bats play a primary role in seed dispersal by carrying the seeds to safe sites, thereby generating

Received June 18, 1998.

H. Godínez-Alvarez,[1] A. Valiente-Banuet, and L. Valiente Banuet. Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70–275, Coyoacán C.P. 04510, México, D.F.

[1] Author to whom all correspondence should be addressed. e-mail: hgodinez@miranda.ecologia.unam.mx

a nonrandom pattern of dispersion (Steenbergh and Lowe 1977; Hutto et al. 1986; Olin et al. 1989; Valiente-Banuet et al. 1996).

In the Tehuacán Valley of south-central Mexico, columnar cacti are the physiognomically dominant elements of the vegetation, which constitutes the densest cacti forest in North America, with 1200 adults/ha (Valiente-Banuet and Ezcurra 1991). The giant columnar cactus *Neobuxbaumia tetetzo* (Coulter) Backeberg is the dominant species of a vegetation type locally called "tetechera," which occupies ca. 400 km^2 in the Valley (Valiente-Banuet et al. 1996). This species is primarily restricted to hillslopes of varying aspect with soils derived mainly from shale and occasionally from limestone. It presents a spatial association to shrubs, and its reproduction and successful seedling establishment depend on the interactions established with different species of bats and birds as well as with nurse plants (Valiente-Banuet and Ezcurra 1991; Valiente-Banuet et al. 1991*b*, 1996). The presence of a heterogeneous landscape and the biotic interactions with other organisms may have a profound effect upon seed germination, seedling establishment, and growth of *N. tetetzo* individuals, therefore affecting its population dynamics.

The purpose of this study is to determine the finite rate of increase and the critical stages of the life cycle of the long-lived *N. tetetzo*, in a semiarid zone of Mexico. By conducting an elasticity analysis and by knowing the biotic interactions occurring in the different life-cycle stages, we can assess the possible role of biotic interactions on its population dynamics.

Materials and methods

Study site and natural history of *N. tetetzo*

The study was conducted in the semiarid Valley of Zapotitlán (18°20'N, 97°28'W), a local basin of the Tehuacán Valley in the state of Puebla, Mexico. This region owes its aridity to the rain shadow produced by the Eastern Sierra Madre (Smith 1965). It has an average rainfall of 380 mm and an annual mean temperature of 21°C with rare frosts (García 1973). Topographically the area is heterogeneous with hills and mountains dominating the landscape. Flat zones are common only on alluvial deposits along Río Salado. Geologically the study zone is covered by a great amount of different lithologies, which include shale, limestone, and igneous materials (Brunet 1967). The main vegetation type is an arid tropical scrub (Rzedowski 1978) in which giant columnar cacti constitute dominant elements of the vegetation. The study was conducted in a zone located around Cerro Cutá, inside the Botanical Garden, located approximately 30 km south of the city of Tehuacán.

Neobuxbaumia tetetzo, an endemic branched columnar cactus that reaches 8 m in height, is the dominant species in the study zone with densities of ca. 1200 individuals/ha (adults were arbitrarily defined as individuals >1 m tall; Valiente-Banuet and Ezcurra 1991). Seed germination and seedling establishment occurs mostly beneath the canopies of several species of trees and shrubs, such as the legumes *Mimosa luisana* Brandegee, *Caesalpinia melanadenia* (Rose) Standley, and *Senna wislizenii* (A. Gray) Irwin & Barneby, producing an association of the species to shrubs (Valiente-Banuet et al. 1991*b*). The growth period is restricted to the rainy season, from June to September (Núñez 1993). First reproduction occurs when plants are around 2 m tall (Valiente-Banuet and Ezcurra 1991). Flowering and fruiting seasons occur from mid-May until the end of June, just before the rainy season. The species is hermaphroditic, and its flowers are whitish and mainly nocturnal, opening at dusk (20:00) and closing in the early morning (06:00). The bats *Choeronycteris mexicana* Tschudi and *Leptonycteris curasoae* Miller are the only pollinators that promote seed production (Valiente-Banuet et al. 1996). Fruits are whitish and open while still on the plant during the night, being consumed by the bats *L. curasoae*, *C. mexicana*, and *Artibeus jamaicensis* Leach. During the day, fruits are consumed by the birds *Columbina inca* Lesson, *Zenaida asiatica* L., *Zenaida macroura* L., *Carpodacus mexicanus* P.L.S. Muller, *Mimus polyglottos* L., *Phainopepla nitens* Swainson, and *Melanerpes hypopolius* Wagler (Valiente-Banuet et al. 1996). Fallen seeds are eaten by ants (*Pogonomyrmex* spp.) and birds (*C. inca*, *Z. asiatica*, and *Z. macroura*; Valiente-Banuet and Ezcurra 1991).

Field methods

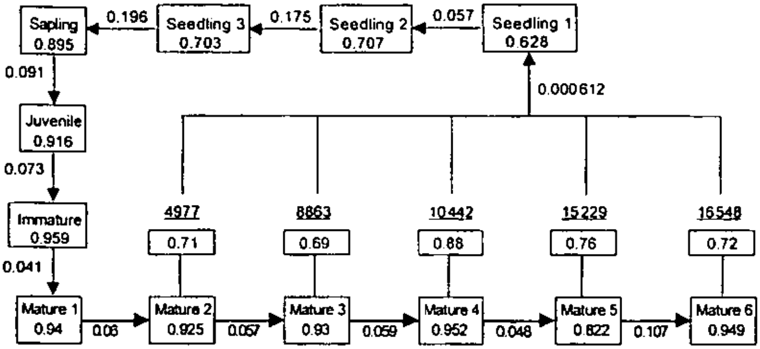
During the dry season in March and April of 1988, a total of 1900 individuals of *N. tetetzo* were tagged in four quadrats of 2000 m^2 each located in slopes with north, east, west, and south aspects. The height of the principal trunk was measured with a levelling rod and size categories were determined following ontogenetic stages and its association with nurse plants as follows: 0–2 cm, seedling 1; 2–8 cm, seedling 2; 8–15 cm, seedling 3; 15–45 cm, sapling; 45–100 cm, juvenile; 100–150 cm, immature; 150–250 cm, mature 1; 250–350 cm, mature 2; 350–450 cm, mature 3; 450–550 cm, mature 4; 550–650 cm, mature 5; ≥650 cm, mature 6. Size categories of seedling, sapling, juvenile, immature, and mature 1 are mostly associated with nurse plants, whereas the other mature categories grow isolated with respect to trees and shrubs. Mature 1 category includes individuals that reached the first reproduction event, although they presented very low reproduction probabilities.

During March of 1989 and 1990, new censuses were conducted to determine the transition probabilities among categories by obtaining the proportion of individuals that passed from one category to the next in 1 year.

Estimations of seed germination and seedling establishment probabilities were obtained experimentally in the study area. The treatments followed a two by two factorial design in which seeds of *N. tetetzo* were sown in open spaces and beneath the canopy of *Mimosa luisana*, the most common nurse plant in the Tehuacán Valley (Valiente-Banuet et al. 1991*a*); and excluded and nonexcluded from predators. Seeds were obtained from ripe, open fruits, and the fleshy mesocarp was dried and removed before sowing. Each experimental unit consisted of 180 seeds sown in a 30 × 30 cm plot and 12 replicates were performed for each treatment. The soil surface was cleaned of other seeds and cactus seedlings and the seeds were sown directly on the surface. Rodents and birds were excluded by completely covering the experimental unit with a 12 mm wire mesh with the bottom edges buried in the soil to a depth of 10 cm. Insects such as ants were excluded using an insecticide powder ("Clordane"). With the number of survivors after 2 years in open spaces and beneath the canopy of *M. luisana* in the nonexcluded treatments, the probability of passing from seed to seedling was calculated assuming a random dispersion in which the proportions of soil covered by shrubs (88.1%) and deprived of vegetation (11.9%) were considered (Valiente-Banuet et al. 1991*a*).

During May and June of 1988, a total of 20 individuals per mature category size were selected at random to determine the mean number of seeds produced. For all the individuals ≥200 cm in height, the probability of reproduction was obtained as the proportion of individuals that produced fruits during the flowering and fruiting time. Because seeds germinate during the rainy season of the same year and no seed bank has been detected, fecundity values were obtained as the product of the probability of reproduction, mean number of seeds produced per size category, and probability of passing from seed to seedling. Additionally these values were

Fig. 1. Life cycle diagram for *Neobuxbaumia tetetzo* growing in Tehuacán Valley, Mexico. Values inside the boxes are survival probabilities, whereas arrows represent transition probabilities between size categories. Boxes above the reproductive categories, from mature 2 to mature 6, are reproduction probabilities. Underlined values are the mean number of seeds produced per size category.



multiplied by the probability that a seedling grow to a height of 1 cm (0.1038, i.e., the middle point of the seedling 1 category).

The model

To obtain the finite rate of increase (λ) of *N. tetetzo*, we constructed a matrix model (Caswell 1989). This model consists basically of a projection matrix (A) and a vector (v). The A matrix is conformed by three principal parts: (*i*) the first row refers to fecundity values for all reproductive stages; (*ii*) the principal diagonal defines probabilities of stasis or proportions of individuals in stage class *i* that remain in the same class after one time interval; and (*iii*) the first lower subdiagonal defines transition probabilities or proportion of individuals in stage class *i* that grow to the next class. The v vector defines the number of individuals in the population for each stage class at time *t*. When the matrix A is multiplied by the vector v one can obtain the population vector at time $t + 1$. If this matrix multiplication is repeated the population rate of increase and the relative abundance in each stage class will become stable. At this point it is possible to estimate demographic parameters such as the finite rate of increase or λ (largest positive eigenvalue), the stable size distribution (right eigenvector), and the reproductive values (left eigenvector; De Kroon et al. 1986; Caswell 1989; Silvertown et al. 1993).

Confidence limits of λ

Confidence limits (90%) were obtained by using Monte Carlo simulation models as proposed by Alvarez-Buylla and Slatkin (1993). The variances for all the matrix entries were estimated assuming a lognormal distribution of errors for fecundity values and a multinomial distribution of errors for transition probabilities. With these assumptions, 1000 simulations were estimated and the sampling distribution of λ was constructed. Confidence limits were determined considering the values of the 5 and 95 percentiles.

Elasticity analysis

An elasticity analysis was performed to determine the most critical stages of the life cycle. Elasticity is a measure of the relative change in the population finite rate of increase in response to small changes in the value of a matrix element (Silvertown et al. 1993). Additionally, we estimated the relative contributions of survival, growth, and fecundity to the finite rate of increase following the methodology proposed by Silvertown et al. (1993). All parameters were estimated with the program STAGECOACH version 2.3.

With transition probabilities and fecundity values for both years, 1988 and 1989, an average projection matrix was constructed and iterated to estimate the stable size distribution and finite rate of increase. The stable size distribution predicted by the model was compared with the actual distribution of individuals in size categories using a *G* test (Sokal and Rohlf 1981).

Results

Life cycle

A life cycle diagram for *N. tetetzo* growing in the Tehuacán Valley is shown in Fig. 1. Seeds presented the lowest survival probability (6.12×10^{-4}) because only 3 of 2160 seedlings were alive in nonexcluded treatments beneath the canopies of *M. luisana*, at the end of the establishment experiment. In contrast, none of the seedlings sown in open spaces survived for more than 60 days. Observations made during the establishment experiment showed that predation by the birds *Columba livia* Gmelin, *Columbina inca*, *Columbina passerina* L., *Z. asiatica*, *Z. macroura*, and the harvester ants (*Pogonomyrmex* spp.) was the principal mortality factor of seeds, whereas seedling mortality was mostly related to the effect of direct solar radiation. Survival probabilities increased for the rest of the size categories.

The proportion of individuals that changed from one category to the next after a 1-year period was low, ranging from 4.1% for immature cactus to 19.6% for individuals of the seedling 3 category.

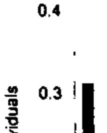
The probability of reproduction was higher for mature 4 individuals (0.88) and decreased for the rest of the reproductive categories. Individual fecundity increased with size, and hence, the number of seeds produced by individuals of the first reproductive category (mature 2) was lower than the number of seeds produced by the other reproductive categories (mature 3 to mature 6).

Finite rate of increase and stable size distribution

Population finite rate of increase estimated by the model was 1.0 with 90% confidence limits of 0.94 and 1.01, indicating that this estimate does not differ from unity.

Stable size distribution predicted by the model differed from the actual size distribution of individuals (Fig. 2). The proportion of individuals in the seedling 1 and immature categories predicted by the model was always greater than the

Fig. 2. Proportion of individuals per size category in stable (solid bars) and actual (open bars) distributions of *Neobuxbaumia tetetzo*. Differences between the two distributions are statistically significant (G = 1467, df 11, $p < 0.000\,01$). se1–se3, seedlings; sa, saplings; j, juveniles; im, immature individuals; m1–m6, mature individuals.



proportion of individuals in those categories in the field. In contrast, the proportion of individuals in the seedling 2, seedling 3, sapling, and juvenile categories observed in the field was greater than the proportion predicted by the model. All these differences were statistically significant (G = 1467, df = 11, $p < 0.000\,01$).

Elasticity analysis

Overall survivorship (91.4%) was the most important life-history parameter that affected the finite rate of increase, followed by growth (7.8%) and fecundity (0.8%). Elasticity values for the survivorship of the first categories increased with size ranging from 1.43% for seedling 1 to 19.82% for immature individuals. In contrast, survivorship elasticity values for the rest of the categories decreased with size, excepting those of the mature 4 category (Table 1).

Among transition probabilities the highest elasticity occurred in seedlings, saplings, juveniles, immatures, and individuals of the first mature category. Elasticity values for the rest of the categories were lower and decreased with size.

Fecundity presented the lowest elasticity values and differed by almost one order of magnitude with respect to survivorship values. Individual fecundity of the mature 4 reproductive category affected λ in greater proportion than fecundity of the other categories (Table 1).

Discussion

Different studies on biotic interactions conducted in deserts have indicated that, among flowering plants, the Cactaceae is a group that strongly interact with organisms of other species along its life cycle for seed production, seedling establishment, and seed dispersal (Steenbergh and Lowe 1969, 1977; Gibson and Nobel 1986; McAuliffe 1988; Valiente-Banuet et al. 1991*a*, 1996, 1997*a*, 1997*b*). However, no studies have determined the role of these interspecific interactions on the population dynamics of cacti.
Elasticity analysis of *N. tetetzo* showed that survivorship
individuals belonging to the categories of saplings, juv
niles, and immature individuals as well as the first reprodu
tive categories (mature 1 to mature 4) are the most importa
stages that affect the population dynamics of this speci
these observations are similar to what has been reported f
the Saguaro (*Carnegiea gigantea* (Engelm.) Britt. & Ros
in the Sonoran Desert (Steenbergh and Lowe 1969, 197
McAuliffe 1984*b*). All of the young and pre-reproducti
size categories of *N. tetetzo* are associated with nurse plan
(Valiente-Banuet et al. 1991*a*), and because columnar ca
are slow growing plants with low transition probabilities, t
importance of nurse plants on survivorship of cacti is relat
to the amelioration of the physical and biotic conditions ne
to the soil surface (Turner et al. 1966; Steenbergh and Lo
1969, 1977; Nobel 1988). Survivorship of the reproducti
categories is affected by the competitive interactions for w
ter established with the nurse plants (Valiente-Banuet et
1991*b*).

Results on seed germination and seedling establishme
experiment indicated that survival and transition probabi
ties of the early seedling stages are low (6.12×10^{-4}) a
highly variable (see seedling 1–3 categories in Fig. 1). A
though our elasticity analysis showed that the values f
these categories are not important for the population dyna
ics of *N. tetetzo*, it is possible that, under natural conditio
these stages of the life cycle play an outstanding role in t
population regulation because of their high variance. Prote
tion against direct solar radiation, extreme temperatures, a
soil moisture evaporation, as well as predators (Shreve 193
Turner et al. 1966; Steenbergh and Lowe 1969, 197
McAuliffe 1984*a*; Franco and Nobel 1989; Valiente-Ban
and Ezcurra 1991) are the main factors that contribute si
nificantly to the survivorship of young individuals
N. tetetzo. Moreover, it has been suggested that the high
nutrient levels found beneath nurse plants may result
faster growth rates that may increase the probability of see
ling survival by allowing a more rapid escape from the cri
cal stages of early growth (Jordan and Nobel 1981; Valien
Banuet and Ezcurra 1991; Godínez-Alvarez and Valien
Banuet 1998).

The successful establishment of seedlings beneath
canopies of perennial nurse plants also emphasizes the re
tive importance of seed dispersal on population dynami
(Turner et al. 1966; Hutto et al. 1986; Valiente-Banuet a
Ezcurra 1991; Valiente-Banuet et al. 1996). The fruits
N. tetetzo are consumed by several species of birds and b
(Valiente-Banuet et al. 1996) suggesting that the hypothe
of directed dispersal to sites located beneath the canopies
trees and shrubs needs to be evaluated, in order to assess
role on the cactus population dynamics (Valiente-Ban
et al. 1996). Studies made with other columnar cactus su
as *C. gigantea*, indicate that birds play an important r
in seed dispersal to safe microsites with environmen
conditions favourable to germination and establishm
(Steenbergh and Lowe 1977; Hutto et al. 1986; Olin et
1989).

Although the estimated finite rate of increase does not d
fer from unity, differences between the actual and predict
stable size distributions indicate that λ does not well rep
sent the current population dynamics of this species. Fi

Table 1. Elasticity matrix for *Neobuxbaumia tetetzo* growing in the Tehuacán Valley, Mexico.

	se1	se2	se3	sa	j	im	m1	m2	m3	m4	m5	m6
se1	1.43							0.11	0.16	0.28	0.1	0.21
se2	0.85	2.04										
se3		0.85	2.00									
sa			0.85	7.18								
j				0.84	9.14							
im					0.85	19.82						
m1						0.85	13.16					
m2							0.85	10.33				
m3								0.74	9.74			
m4									0.58	11.4		
m5										0.3	1.39	
m6											0.21	3.79

Note: Elasticity values were multiplied by 100 to be represented as percentages. Size categories are as follows: se1–se3, seedlings; sa, saplings; j, juveniles; im, immature individuals; m1–m6, mature individuals.

observations indicate that there is a high variability in the reproductive behaviour of populations among years. For instance, in a period of 1–3 years, less than 10% of the reproductive individuals could produce flowers or even its reproduction may fail. Long-term studies are necessary to determine what other factors are influencing the population dynamics of *N. tetetzo*.

From all our results we can conclude that *N. tetetzo* is a species with a high mortality in the young size categories that decreases in older stages. During the initial phases of the life cycle and specifically during the young phases, their association to nurse plants emphasize the role of seed dispersal by bats and birds and also the role of positive interactions on population dynamics of this long-lived cactus species.

Acknowledgements

Miguel Verdú and Saleem Dar made valuable comments on the first draft of the manuscript. This study was supported by the Dirección General de Asuntos del Personal Académico de la UNAM (DGAPA IN-208195) and Fondo Mexicano para la Conservación de la Naturaleza (FMCN) Project A-1-97/36.

References

Alvarez-Buylla, E., and Slatkin, M. 1993. Finding confidence limits on population growth rates: Monte Carlo test of a simple analytic method. Oikos, **68**: 273–282.

Brunet, J. 1967. Geologic studies. *In* The prehistory of the Tehuacan Valley. Vol. 1. Environment and subsistence. *Edited by* D.S. Byers. University of Texas Press, Austin, Tex. pp. 66–90.

Caswell, H. 1989. Matrix population models. Construction, analysis and interpretation. Sinauer Associates, Sunderland, Mass.

De Kroon, H., Plaiser, A., van Groenendael, J., and Caswell, H. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology, **67**: 1427–1431.

Franco, A.C., and Nobel, P.S. 1989. Effect of nurse plants on the microhabitat and growth of cacti. J. Ecol. **77**: 870–886.

García, E. 1973. Modificaciones al sistema de clasificación climática de Köppen. Instituto de Geografía, Universidad Nacional Autónoma de México, México.

Gibson, A.C., and Nobel, P.S. 1986. The cactus primer. Harvard University Press, Cambridge, Mass.

Godínez-Alvarez, H., and Valiente-Banuet, A. 1998. Germination and early seedling growth of Tehuacán Valley cacti species: the role of seed ingestion by dispersers and soils on seedling growth. J. Arid Environ. **39**: 21–31.

Harper, J.L. 1977. Population biology of plants. Academic Press, New York.

Hutto, R.L., McAuliffe, J.R., and Hogan, L. 1986. Distributional associates of the saguaro (*Carnegiea gigantea*). Southwest. Nat. **31**: 469–473.

Jordan, W.P., and Nobel, P.S. 1981. Seedling establishment of *Ferocactus acanthodes* in relation to drought. Ecology, **62**: 901–906.

McAuliffe, J. 1984*a*. Prey refugia and the distributions of two Sonoran desert cacti. Oecologia, **65**: 82–85.

McAuliffe, J. 1984*b*. Sahuaro – nurse tree associations in the Sonoran desert: competitive effects of Sahuaros. Oecologia, **64**: 319–321.

McAuliffe, J. 1986. Herbivore-limited establishment of a Sonoran desert tree, *Cercidium microphyllum*. Ecology, **67**: 276–280.

McAuliffe, J. 1988. Markovian dynamics of simple and complex desert plant communities. Am. Nat. **131**: 459–490.

Niering, W.A., Whittaker, R.H., and Lowe, C.H. 1963. The saguaro: a population in relation to environment. Science (Washington, D.C.), **142**: 15–23.

Nobel, P.S. 1988. Environmental biology of agaves and cacti. Cambridge University Press, New York.

Núñez, H. 1993. Determinación de edades de una cactácea columnar gigante *Neobuxbaumia tetetzo* (Coulter) Backeberg, en Zapotitlán de las Salinas, Puebla. Bachelors thesis, Universidad Nacional Autónoma de México, México, D.F.

Olin, G., Alcorn, S.M., and Alcorn, J.M. 1989. Dispersal of viable saguaro seeds by white-winged dove (*Zenaida asiatica*). Southwest. Nat. **34**: 282–284.

Rzedowski, J. 1978. Vegetación de México. Editorial Limusa, México.

Shreve, F. 1931. Physical conditions in sun and shade. Ecology, **12**: 96–104.

Silvertown, J.W., Franco, M., Pisanty, I., and Mendoza, A. 1993. Comparative plant demography-relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. J. Ecol. **81**: 465–476.

Smith, C.E. 1965. Flora of Tehuacan Valley. Fieldiana Bot. **31**: 107–143.

Sokal, R.R., and Rohlf, F.J. 1981. Biometry. W.H. Freeman & Co., New York.

Steenbergh, W.H., and Lowe, C.H. 1969. Critical factors during the first years of life of the saguaro (*Cereus giganteus*) at the Saguaro National Monument, Arizona. Ecology, **50**: 825–834.

Steenbergh, W.H., and Lowe, C.H. 1977. Ecology of the Saguaro: II. Reproduction, germination, establishment, growth and survival of the young plant. U. S. Government Printing Office, Washington, D.C. Natl. Park Serv. Sci. Monogr. Ser. No. 8.

Turner, R.M., Alcorn, S.M, Olin, G., and Booth, J.A. 1966. The influence of shade, soil and water on saguaro seedling establishment. Bot. Gaz. **127**: 95–102.

Valiente-Banuet, A., and Ezcurra, E. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán Valley, Mexico. J. Ecol. **79**: 961–971.

Valiente-Banuet, A., Vite, G.F., and Zavala-Hurtado, A. 1991*a*. *Interaction between the cactus Neobuxbaumia tetetzo* and the nurse shrub *Mimosa luisana*. J. Veg. Sci. **2**: 12–14.

Valiente-Banuet, A., Briones, O., Bolongaro-Crevenna, A., Ezcurra, E., Rosas, M., Núñez, H., Barnard, G., and Vázquez, E. 1991*b*. Spatial relationships between cacti and nurse shrubs in a semi-arid environment in central Mexico. J. Veg. Sci. **2**: 15–20.

Valiente-Banuet, A., Arizmendi, M. del C., Rojas-Martínez, A., and Domínguez-Canseco, L. 1996. Ecological relationships between columnar cacti and nectar feeding bats in Mexico. J. Trop. Ecol. **12**: 103–119.

Valiente-Banuet, A., Rojas-Martínez, A., Arizmendi, M. del C., and Dávila, P. 1997*a*. Pollination biology of two columnar cacti (*Neobuxbaumia mezcalaensis* and *Neobuxbaumia macrocephala*) in the Tehuacan Valley, central Mexico. Am. J. Bot. **84**(4): 452–455.

Valiente-Banuet, A., Rojas-Martínez, A., Casas, A., Arizmendi, M. del C., and Dávila, P. 1997*b*. Pollination biology of two winter-blooming giant columnar cacti in the Tehuacán Valley, central Mexico. J. Arid Environ. **37**: 331–341.

Journal of Arid Environments (1998) 39: 21–31
Article No. ae980376

Germination and early seedling growth of Tehuacan Valley cacti species: the role of soils and seed ingestion by dispersers on seedling growth

Héctor Godínez-Alvarez & Alfonso Valiente-Banuet

Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275, C.P. 04510, México, D.F.

(*Received 10 November 1997, accepted 23 January 1998*)

This study determined the effect of imbibition, temperature, and mechanical and acid scarification on germination of eight cacti species, simulating seed ingestion by birds and bats. The effect of shading and soils on seedling growth of two columnar species was also analysed, considering environmental modifications produced by nurse plants. Only *Pachycereus hollianus* increased its germination after seeds were soaked in acid solutions, whereas for the other species none of the treatments increased their germination. Shading affected the growth of *Neobuxbaumia tetetzo* seedlings, whereas soils beneath nurse plants increased seedling growth of *P. hollianus*, indicating that soils help survival through early-critical stages.

Keywords: Cactaceae; establishment; seed dispersal; seed germination; seedling growth; shading; soil; nurse plants

Introduction

Studies on seed germination and seedling establishment of cacti have shown that these critical phases of the life cycle (Steenbergh & Lowe, 1969, 1977) occur beneath the canopies of perennial nurse plants (Turner *et al.*, 1966; Steenbergh & Lowe, 1969, 1977; Valiente-Banuet *et al.*, 1991*a*). Because the canopies of nurse plants usually do not form a continuous layer in arid zones, this recruitment pattern depends strongly on seed dispersal by animals to those vegetation patches, and on the microenvironmental modifications produced by trees and shrubs enhancing seed germination and early seedling survivorship (Valiente-Banuet & Ezcurra, 1991). Thus, nurse plants provide protection against direct solar radiation, extreme temperatures and soil moisture evaporation (Shreve, 1931; Turner *et al.*, 1966; Steenbergh & Lowe, 1969, 1977; Franco & Nobel, 1989; Valiente-Banuet & Ezcurra, 1991). Moreover, it has been reported also that nurse plants increase soil nitrogen levels under their canopies (García-Moya & McKell, 1970), modifying the growth rates of seedlings and increasing their survival probability by allowing a more rapid escape from the critical stages of early growth (Jordan & Nobel, 1981; Valiente-Banuet & Ezcurra, 1991).

0140–1963/98/010021 + 11 $30.00/0

In the Tehuacan Valley, located in south-central Mexico, fruits of cacti are consumed by the birds *Melanerpes hypopolius* Wagler, *Zenaida asiatica* Linnaeus, *Carpodacus mexicanus* P. L. S. Muller, *Mimus polyglottos* Linnaeus and *Phainopepla nitens* Swainson, and also by some species of bats such as *Leptonycteris curasoe* Miller, *Choeronycteris mexicana* Tschudi and *Artibeus jamaicensis* Leach (Valiente-Banuet *et al.*, 1996), and the establishment and growth of all of these cacti species occur associated with trees and shrubs (Valiente-Banuet *et al.*, 1991*a*). Although some studies have determined general underlying mechanisms to explain this pattern in terms of shade and moisture conditions (Turner *et al.*, 1966; Valiente-Banuet & Ezcurra, 1991), it is unknown if seed ingestion by dispersers plays an important role in germination. Recent studies have indicated that seed germination in cacti increases when the seeds are ingested by lizards and birds (León de la Luz & Domínguez Cadena, 1991; Côrtes Figueira *et al.*, 1994), when soaked in acid solutions (Nolasco *et al.*, 1996), or when imbibed for different periods (Alcorn & Kurtz, 1959; McDonough, 1964). These results suggest that seed treatments provided by dispersers may play an important role in the establishment phase of cacti (Howe, 1986; Izhaki & Safriel, 1990; Schupp, 1993).

The present study aims to ascertain threshold conditions for seed germination of eight cacti species that inhabit the Tehuacan Valley, located in south-central Mexico, recognized as a centre of endemism and diversity of cacti (Valiente-Banuet *et al.*, 1996). These cacti species embrace an ample variety of growth forms within the cactus family (Gibson & Nobel, 1986) including the globose cacti *Coryphantha pallida* Britton & Rose, *Echinocactus platyacanthus* Link & Otto, and *Ferocactus flavovirens* (Scheidw.) Britton & Rose; the columnar cacti *Myrtillocactus geometrizans* (Mart.) Console, *Neobuxbaumia tetetzo* (Coult.) Backeb. and *Pachycereus hollianus* (Weber) Buxb.; and the opuntioid species *Opuntia puberula* Pfeiff. The effects of temperature, imbibition, and mechanical and acid scarification on seed germination were analysed, simulating the differences in temperature found under shrubs and openings (Valiente-Banuet *et al.*, 1991*a*), the effect of gizzards on seeds when ingested by birds (Olin *et al.*, 1989) and the acidic conditions found in the digestive tract of birds and mammals (Howell, 1974).

Additionally, a seedling growth experiment was conducted with two columnar cacti, *Neobuxbaumia tetetzo* and *Pachycereus hollianus*, to test the role of nutrient-enriched soils found beneath the canopies of the legume *Mimosa luisana* Brandegee, the most common nurse plant in the Tehuacan Valley (Valiente-Banuet *et al.*, 1991*b*), considering that the mean total nitrogen content of soils beneath the canopy of this species (0·22 ± 0·002%, mean ± 1 SE) and in openings (0·19 ± 0·001%) differs significantly (Valiente-Banuet *et al.*, 1991*b*).

Materials and methods

Germination

Seeds of all the species studied were obtained from mature fruits randomly collected from plants growing in the Helia Bravo Botanical Garden (18° 20′ N, 97° 28′ W), located approximately 30 km south of the city of Tehuacan in the state of Puebla, Mexico. Collected fruits were dried at room temperature and seeds were separated by dissection and washed with tap water to remove any remaining pulp. Seeds were dried on absorbent paper before placing them into glass containers for storing at room temperature in a fresh, dry place for a few days until experiments were carried out.

A total of four experiments were conducted independently in a one-way analysis of variance design and compared against a control treatment consisting of seeds sown in Petri dishes with 1% agar: (1) *acid immersion experiment*: seeds were immersed in hydrochloric acid solutions of pH 1, 2, 3 and 6 for 1 h. After treatment, seeds were washed with tap water and sown in Petri dishes; (2) *imbibition experiment*: seeds were placed in glass containers with tap water for 12, 24 and 48 h, and then sown in Petri dishes; (3) *temperature experiment*: seeds were maintained in an environmental chamber with either constant temperature of 17°C, fluorescent light and a photoperiod of 12 h light/12 h dark, or with fluctuating temperature of 20–25°C, fluorescent light and a photoperiod of 12 h light/12 h dark. The temperature in this chamber increased 2°C every 2 h from 0800h until 1200h. At 1400h, temperature reached its maximum (25°C) and then decreased 2°C every 2 h until a temperature of 20°C at 2000h; (4) *scarification experiment*: seeds were rubbed with sandpaper almost until the seed coat was cracked.

All germination experiments, except those on temperature, were performed at laboratory room temperature (15–23°C) and natural daylight conditions. Seeds were disinfected by immersion in 5% sodium hypochlorite for 5 min and sown in Petri dishes with 1% agar. Fifty seeds per plate were used and four replicates were performed for each treatment. Petri dishes were sealed with adhesive tape and germinated seeds were counted every 3 days for a period of 20 to 25 days. The criterion used to consider a seed germinated was radicle emergence from the embryo. The proportion of germinated seeds in each of the four experiments were arcsine transformed and analysed using a one-way analysis of variance to compare the effect of each treatment on seed germination with the control treatment of the eight cacti species. Null hypothesis considered an equal number of germinated seeds between the treatment and control.

Seedling growth

An experiment to assess the effect of shading and different soil types on seedling growth of *Neobuxbaumia tetetzo* and *Pachycereus hollianus* was conducted during 1990. This experiment was performed in a cactus nursery of 200 m^2, located in the Zapotitlán Valley (18° 20' N, 97° 28' W), a local basin of the Tehuacan Valley in the state of Puebla, Mexico. This region owes its aridity to the rain shadow produced by the Sierra Madre Oriental (Valiente-Banuet *et al.*, 1996), and receives an average annual rainfall of 380 mm. Annual mean temperature averages 21°C with very rare frosts. The main vegetation type is an arid tropical scrub (Osorio *et al.*, 1996) in which giant columnar cacti constitute the most important physiognomic elements. The cactus nursery was built of mesquite branches and grass leaves as roof and dry agave flowering stalks as roof support. For each species, a two-way factorial experimental design of two soil types and three levels of shading were used. Soils were extracted from open spaces and beneath the canopies of *M. luisana*. The shading factor consisted of three different conditions, namely cactus nursery ($125 \pm 23\,\mu mol\,m^{-2}\,s^{-1}$ of photosynthetic active radiation (PAR), mean ± standard deviation, $N = 41$; 11–38°C), artificial shading simulating the canopies of *M. luisana* shrubs ($261 \pm 30\,\mu mol\,m^{-2}\,s^{-1}$ of PAR, $N = 41$; 5-43°C), and openings ($1870 \pm 4\,\mu mol\,m^{-2}\,s^{-1}$ of PAR, $N = 41$; 9-43°C). The canopies of *M. luisana* shrubs were simulated using a 1·5 mm green nylon net.

The experimental unit for all treatments consisted of a plastic container in which ten seeds were sown. A total of 42 replicates per treatment were used in order to harvest seven crops of six containers every 2 weeks to measure the dry weight of seedlings. Seedling growth occurred at temperatures ranging from 25 to 43°C and plants were watered every 3 days until field capacity.

Dry weight of seedlings at the end of the experiment (*c.* 150 days) was analysed for each species using a factorial analysis of variance under the null hypothesis that seedling dry weights were equal for the different treatments.

Seedling growth rates for each species were also estimated using a log-linear model, considering time as continuous variable and soil type and shading as discrete variables. The dry weight of seedlings were log-transformed and the analysis was made with the GLIM statistical package version 3.77, considering a normal error and link function identity (Crawley, 1993). The fitted model was: $W_t = a \cdot \exp(bt)$ where, W_t is the dry weight of seedlings at time t, a is the dry weight of seedlings at $t = 0$, and b is the growth rate.

Results

Germination

Acid immersion experiment

Seed germination for all species was a rapid process that occurred within the first 2 to 5 days after the experiment started. The number of germinated seeds in the control treatment varied among species, ranging from 95% in *N. tetetzo* and *C. pallida* to 11% in *O. purrula*. Immersion of seeds in acid solutions of different pH for all species did not increase germination in seven out of the eight species in comparison with the control treatment (Fig. 1). *Pachycereus hollianus* was the only species that presented a significant increase in the number of germinated seeds after immersion in acid solution of pH 1.

Imbibition experiment

Imbibition of seeds in tap water for different periods of time did not increase seed germination compared to the control treatment (Fig. 2). In contrast, the germination percentages of *N. tetetzo* and *M. geometrizans* decreased significantly when their seeds were imbibed for 48 and 24 h, respectively.

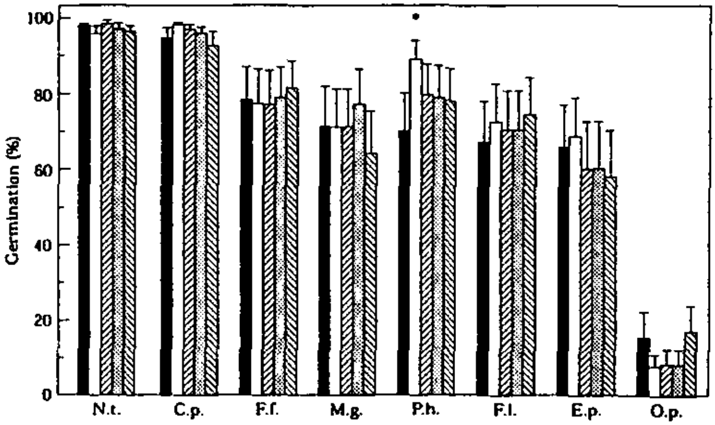


Figure 1. Effect of different acid solutions on seed germination of eight cacti species. Bars marked with an asterisk had significant differences ($p < 0.05$). N.t. = *Neobuxbaumia tetetzo*; C.p. = *Coryphantha pallida*; F.f. = *Ferocactus flavovirens*; M.g. = *Myrtillocactus geometrizans*; P.h. = *Pachycereus hollianus*; F.l. = *Ferocactus latispinus*; E.p. = *Echinocactus platyacanthus*; O.p. = *Opuntia puberula*. (■) = control; (□) = pH 1; (▨) = pH 2; (▒) = pH 3; (▧) = pH 6.

Temperature experiment

The proportion of germinated seeds in five of the eight species maintained at constant temperature (17°C) did not differ from those obtained in fluctuating temperatures (20-25°C). *Ferocactus latispinus*, *E. platyacanthus* and *O. puberula* were the three species in which constant temperature decreased seed germination significantly in comparison to fluctuating temperature (Fig. 3).

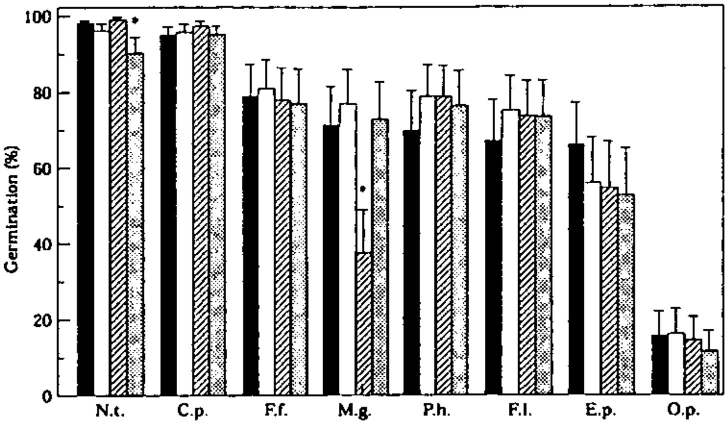


Figure 2. Effect of different imbibiton periods on seed germination of eight cacti species. Bars marked with an asterisk had significant differences ($p < 0.05$). Letters as in Fig. 1. (■) = control; (□) = 12 h; (▨) = 24 h; (▩) = 48 h.

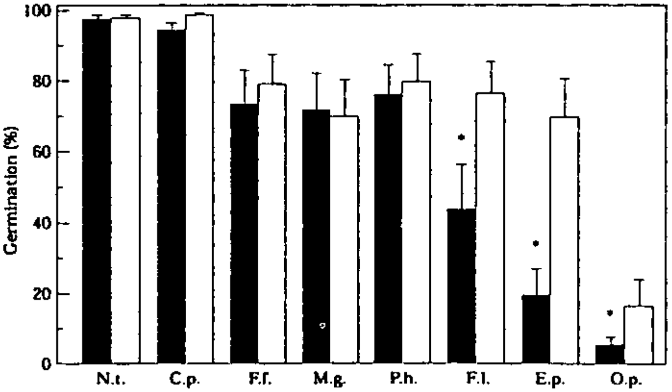


Figure 3. Effect of constant and fluctuating temperatures on seed germination of eight cacti species. Bars marked with an asterisk had significant differences ($p < 0.05$). Letters as in Fig. 1 (■) = 17°C constant; (□) = 20-25°C fluctuating.

Scarification experiment

Scarification treatment decreased seed germination by more than 50% when compared with the control in *N. tetetzo*, *C. pallida*, *F. flavovirens*, *F. latispinus*, *E. platyacanthus* and *O. puberula*; although germination of *M. geometrizans* and *P. hollianus* increased in comparison to the control treatment, these differences were not statistically significant (Fig. 4).

Seedling growth

Seeds sown in open spaces did not germinate and, consequently, these treatments were not considered in further growth analyses. The effect of soils and shading produced contrasting results in the two species considered. *Neobuxbaumia tetetzo* had its highest growth in open-space soils and under shade in the cactus nursery, whereas *P. hollianus* showed enhanced growth in the nurse-plant soil under cactus nursery conditions (Table 1). Of all the factors and interactions, shading explained the highest proportion of the total variance, with 25% for *N. tetetzo* and 54% for *P. hollianus*; the proportion of variance explained by the interaction term varied from 24% in *N. tetetzo* to 2% in *P. hollianus* (Table 2).

The fitted models explained 80% and 86% of the total variance for *N. tetetzo* and *P. hollianus*, respectively. Time and shading were the terms that explained the greatest proportion of the variance (98%), whereas the rest of the factors explained no more than 2%. There were no statistically significant differences in growth rates between all treatments, except seedlings of *P. hollianus* growing in soils from open spaces and artificial shading which presented the lowest growth rates (Table 1; Fig. 5).

Discussion

Seeds of practically all the cacti species germinated rapidly within the first week after sowing only with watering and, therefore, ingestion of seeds by dispersers does not affect germination. Only the seeds of *P. hollianus* significantly increased their

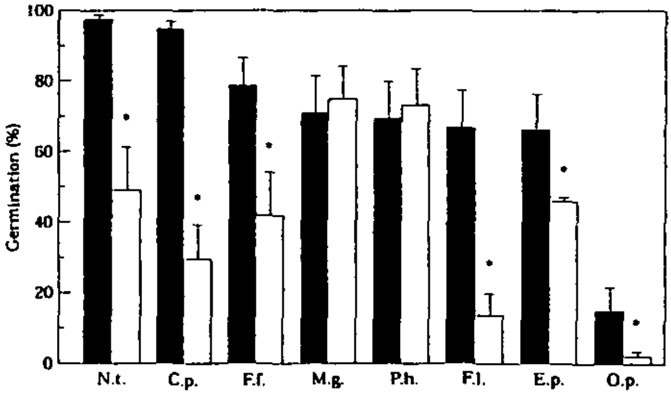


Figure 4. Effect of scarification on seed germination of eight cacti species. Bars marked with an asterisk had significant differences. Letters as in Fig. 1. (■) = control; (□) = scarification.

germination when immersed in an acid solution. Recent studies on seed germination have shown that in the cacti *Pachycereus pringlei* (S. Wats.) Britton & Rose, *Melocactus violaceus* Pfeiff. and *Stenocereus gummosus* (Engelm.) Gibson & Horak, germination increased after seeds were soaked in acid solutions (Nolasco *et al.*, 1996) or ingested by lizards or birds (León de la Luz & Dominguez Cadena, 1991; Côrtes Figueira *et al.*, 1994). Although field observations in the Tehuacan Valley have shown that fruits of the species are consumed by birds and bats (Valiente-Banuet *et al.*, 1996), only *P. hollianus* improves its seed germination after animal ingestion. Consequently, the principal role of seed consumers for most of the species is in seed transportation.

Table 1. *Mean dry weight (mg±standard error) and growth rate (mg day^{-1}) for seedlings of* Neobuxbaumia tetetzo *and* Pachycereus hollianus *growing in different conditions of shading and soil type. Values in parentheses indicate seedling growth rates. Numbers with the same letter did not differ significantly (p<0·05)*

	Soil type	
	Open space	*Mimosa luisana*
Neobuxbaumia tetetzo		
Cactus nursery	18·5±0·5 a	15·4±0·6 b
	(0·014)	(0·012)
Artificial shading	7·6±0·2 c	15·3±1·3 b
	(0·014)	(0·015)
Pachycereus hollianus		
Cactus nursery	25·4±0·9 b	33·4±1·1 a
	(0·016)	(0·016)
Artificial shading	13·8±0·8 c	15·7±1·1 c
	(0·011 a)	(0·016)

Table 2. *Analysis of variance for dry weights (mg) of seedlings of* Neobuxbaumia tetetzo *and* Pachycereus hollianus *growing in different conditions of shading and soil type*

Source of variation	SS	df.	MS	*F*	*p*
Neobuxbaumia tetetzo					
Shading	806·2	1	806·2	63·3	***
Soil type	144·0	1	144·0	11·3	***
Shading×soil type	779·5	1	779·5	61·2	***
Error	1490·0	117	12·7		
Total	3219·7	120			
Pachycereus hollianus					
Shading	4605·5	1	4605·5	146·2	***
Soil type	530·6	1	530·6	16·8	***
Shading×soil type	202·6	1	202·6	6·43	*
Error	3243·6	103	31·5		
Total	8582·3	106			

*p<0·05; ***p<0·0001.

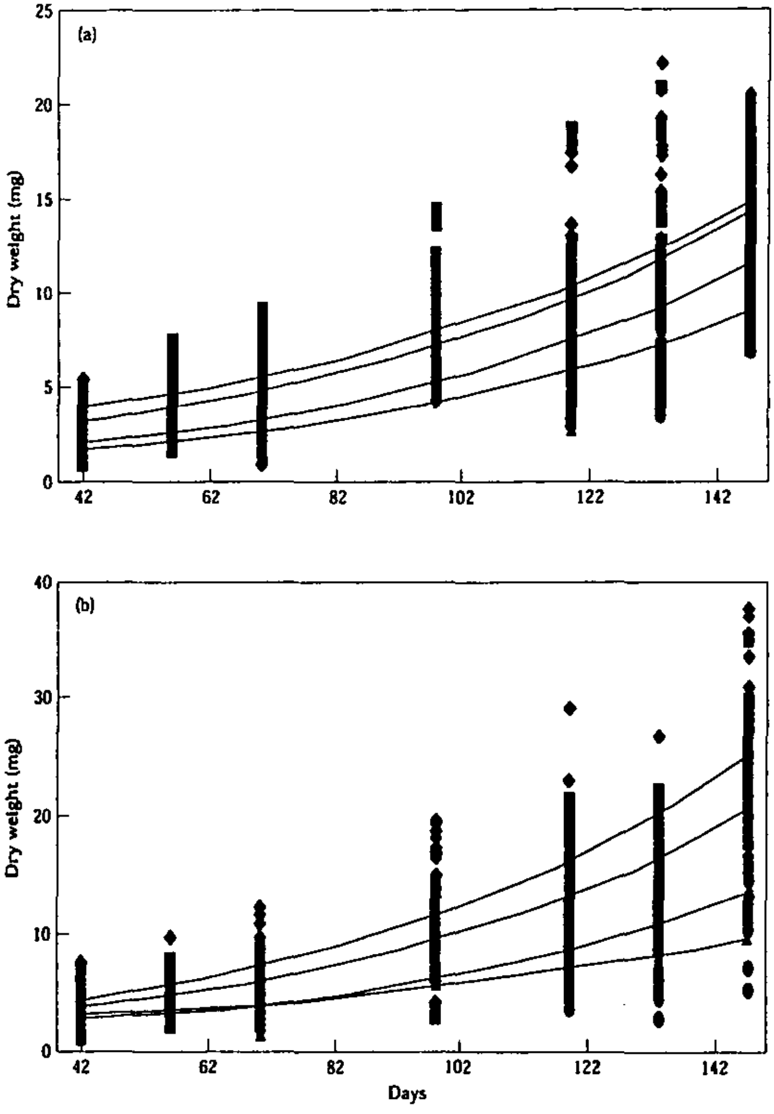


Figure 5. Log-linear models fitted to seedling dry weights of (a) *Neobuxbaumia tetetzo* and (b) *Pachycereus hollianus* growing in different conditions of shading and soil type: (—) = cactus nursery and open-space soils; (······) = cactus nursery and *Mimosa luisana* soils; (- - - - -) = artificial shading and open-space soils, (– - - –) = artificial shading and *Mimosa luisana* soils.

Imbibition of seeds for different periods did not enhance seed germination. These results are in contrast to those reported by Alcorn & Kurtz (1959) and McDonough (1964) in which the seeds of *Carnegiea gigantea* (Engelm.) Britton & Rose and *Stenocereus thurberi* (Engelm.) Buxb. germinated when they were imbibed for a few days. Also, imbibition of *Stenocereus griseus* (Haw.) Buxb. seeds for periods of 24 h favoured germination (Martínez-Holguín, 1983).

Some authors have analysed the effect of temperature on seed germination of cacti. Fearn (1974, 1981) and Nobel (1988) found that germination of several species of cacti occurred in a wide range of temperatures varying from 12 to 34°C. Additionally, Alcorn & Kurtz (1959) reported that constant and fluctuating temperatures did not affect the germination of *C. gigantea* seeds. In this study, temperature treatment did not affect germination. The number of germinated seeds for all species studied, excepting *F. latispinus*, *E. platyacanthus* and *O. puberula*, was similar in constant and fluctuating temperatures.

The lowest germination percentages found in the scarification treatment could be possibly related to damage in the embryos. McDonough (1964) reported that seed germination of *C. gigantea* and *S. thurberi* decreased to 3 and 1%, respectively, after the seed coat was cracked.

Our results indicate that none of the treatments used had a real effect on germination of the seven cacti species studied, suggesting that the seeds of these species, except *O. puberula*, do not present any of the usual physiological dormancy mechanisms. These seeds seem to be resistant to environmental challenge such as temperature fluctuations and ingestion by animals. Seed germination is prevented mostly by environmental factors such as water deficiency and direct solar radiation. Under these conditions seeds do not germinate, even with watering. Valiente-Banuet *et al.* (1991*a*) reported that soil surface temperatures in open spaces reached a maximum of about 40°C at 1400h. Our results are similar to reports for other cacti species such as *C. gigantea* (Turner *et al.*, 1966; Steenbergh & Lowe, 1977) and *S. thurberi* (Nolasco *et al.*, 1997) in which soil moisture availability controls seed germination.

The low germination response found in *O. puberula* was similar to that reported by Pilcher (1970) for other species of *Opuntia*, and suggest that the genus *Opuntia* probably present an embryo dormancy, just as has been reported for *O. phaeacantha* Engelm. var. *major* Engelm. (Pilcher, 1970).

The results on seedling growth of *N. tetetzo* and *P. hollianus* showed that shading has a significant effect on the growth of young cacti individuals. The best conditions for seedling growth were in the cactus nursery in which direct solar radiation decreased 97% with respect to open spaces. These results are similar to those reported by Nolasco *et al.* (1997) in which *S. thurberi* seedlings growing in low solar irradiation and high water availability were bigger and healthier than seedlings growing in other treatments in which solar irradiation was higher.

The higher nutrient levels found beneath the canopies of nurse plants (Valiente-Banuet *et al.*, 1991*b*) resulted in a faster growth rate only for *P. hollianus* seedlings and did not affect the growth of *N. tetetzo*. Different authors have indicated that a faster growth during the seedling stage may increase the survival probability by allowing a more rapid escape from this critical stage (Jordan & Nobel, 1981; Valiente-Banuet & Ezcurra, 1991). Long-term analysis of seedling dry weights are necessary to determine the role of soil nutrient levels in the growth and survivorship of young plants of *N. tetetzo*.

In short, the results found in this study suggest that consumption of seeds by animals in most of the species analysed does not affect their germination and, therefore, soil moisture and the microenvironmental modifications produced by nurse plants play primary roles in seed germination and seedling establishment of cacti. All these results emphasize the role of microenvironmental modifications produced by nurse plants and, consequently, the importance of dispersal of seeds by animal vectors to safe sites for the establishment of cacti under natural conditions.

This study was supported by CONABIO (G-017) and Dirección General de Asuntos del Personal Académico of UNAM (DGAPA IN-208195).

References

Alcorn, S.M. & Kurtz, E.B. (1959). Some factors affecting the germination of seed of the saguaro cactus (*Carnegiea gigantea*). *American Journal of Botany*, **46**: 526–529.

Côrtes Figueira, J.E., Vasconcellos-Netto, J., García, M.A. & Teixeira de Souza, A.L. (1994). Saurocory in *Melocactus violaceus* (*Cactaceae*). *Biotropica*, **26**: 295–301.

Crawley, M.J. (1993). *GLIM for Ecologists*. Cambridge: Blackwell Science. 379 pp.

Fearn, B. (1974). An investigation into the effect of temperature on the seed germination of nine species of cacti using thermal gradient bars. *Cactus and Succulent Journal (U.S.)*, **XLVI**: 214–219.

Fearn, B. (1981). Seed germination: the modern approach. *Cactus and Succulent Journal (G.B.)*, **43**: 13–16.

Franco, A.C. & Nobel, P.S. (1989). Effect of nurse plant on the microhabitat and growth of cacti. *Journal of Ecology*, **77**: 870–866.

García-Moya, E. & McKell, C.M. (1970). Contribution of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology*, **51**: 81–88.

Gibson, A.C. & Nobel, P.S. (1986). *The Cactus Primer*. Cambridge, MA: Harvard University Press. 286 pp.

Howe, H.F. (1986). Seed dispersal by fruit-eating birds and mammals. In: Murray, D. (Ed.), *Seed Dispersal*, pp. 123–189. New York: Academic Press. 322 pp.

Howell, D.J. (1974). Bats and pollen: physiological aspects of the syndrome of chiropterophily. *Comparative Biochemistry and Physiology*, **48**: 263–276.

Izhaki, Y. & Safriel, U.N. (1990). The effect of some mediterranean scrubland frugivores upon germination patterns. *Journal of Ecology*, **78**: 56–65.

Jordan, W.P. & Nobel, P.S. (1981). Seedling establishment of *Ferocactus acanthodes* in relation to drought. *Ecology*, **62**: 901–906.

León de la Luz, J.L. & Domínguez Cadena, R. (1991). Evaluación de la reproducción por semilla de la pitaya agria (*Stenocereus gummosus*) en Baja California Sur, Mexico. *Acta Botánica Mexicana*, **14**: 75–87.

Martínez-Holguín, E. (1983). Germinación de semillas de *Stenocereus griseus* (Haw.) Buxbaum (Pitayo de Mayo). *Cactáceas y Suculentas Mexicanas*, **28**: 51–57.

McDonough, W.T. (1964). Germination responses of *Carnegiea gigantea* and *Lemaireocereus thurberi*. *Ecology*, **45**: 155–159.

Nobel, P.S. (1988). *Environmental Biology of Agaves and Cacti*. New York: Cambridge University Press. 270 pp.

Nolasco, H., Vega-Villasante, F., Romero-Schmidt, H.L. & Diaz-Rondero, A. (1996). The effects of salinity, acidity, light and temperature on the germination of seeds of cardón (*Pachycereus pringlei* (S. Wats.) Britton & Rose, *Cactaceae*). *Journal of Arid Environments*, **33**: 87–94.

Nolasco, H., Vega-Villasante, F. & Diaz-Rondero, A. (1997). Seed germination of *Stenocereus thurberi* (*Cactaceae*) under different solar irradiation levels. *Journal of Arid Environments*, **36**: 123–132.

Olin, G., Alcorn, S.M. & Alcorn, J.M. (1989). Dispersal of viable saguaro seeds by white-winged doves (*Zenaida asiatica*). *Southwestern Naturalist*, **34**: 282–284.

Osorio, O., Valiente-Banuet, A., Dávila, P. & Medina, R. (1996). Tipos de vegetación y diversidad β en el Valle de Zapotitlán de las Salinas, Puebla. *Boletín de la Sociedad Botánica de México*, **59**: 35–58.

Pilcher, B.L. (1970). Germination of seeds of four species of *Opuntia*. *Cactus and Succulent Journal of America*, **42**: 281–282.

Schupp, E.W. (1993). Quantity, quality and the effectiveness of seed dispersed by animals. *Vegetatio*, **107/108**: 15–29.

Shreve, F. (1931). Physical conditions in sun and shade. *Ecology*, **2**: 96–104.

Steenbergh, W.F. & Lowe, C.H. (1969). Critical factors during the first years of life of the saguaro (*Cereus giganteus*) at Saguaro National Monument, Arizona. *Ecology*, **50**: 825–834.

Steenbergh, W.F. & Lowe, C.H. (1977). *Ecology of the Saguaro: II Reproduction, germination establishment, growth and survival of the young plant.* National Park Service Scientific Monograph Series, Number 8. Washington, DC: U.S. Government Printing Office. 242 pp.

Turner, R.M., Alcorn, S.M., Olin, G. & Booth, J.A. (1966). The influence of shade, soil and water on saguaro seedling establishment. *Botainical Gazette*, **127**: 95–102.

Valiente-Banuet, A. & Ezcurra, E. (1991). Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse-plant *Mimosa luisana* in the Tehuacan Valley, Mexico. *Journal of Ecology*, **79**: 961–971.

Valiente-Banuet, A., Bolongaro-Crevenna, A., Briones, O., Ezcurra, E., Rosas, M., Núñez, H., Barnard, G. & Vázquez, E. (1991a). Spatial relationships between cacti and nurse shrubs in a semi-arid environment in central Mexico. *Journal of Vegetation Science*, **2**: 15–20.

Valiente-Banuet, A., Vite, F. & Zavala-Hurtado, J.A. (1991b). Interaction between the cactus *Neobuxbaumia tetetzo* and the nurse shrub *Mimosa luisana*. *Journal of Vegetation Science*, **2**: 11–14.

Valiente-Banuet, A., Arizmendi, M. del, C., Rojas-Martínez, A. & Domínguez-Canseco, L. (1996). Ecological relationships between columnar cacti and nectar feeding bats in Mexico. *Journal of Tropical Ecology*, **12**: 103–119.

LRH: Godínez-Alvarez and Valiente-Banuet

Fruit-Feeding Behavior of *Leptonycteris curasoae* and *Choeronycteris mexicana* in Flight Cage Experiments: Consequences for Dispersal of Columnar Cactus Seeds[1]

---

[1] Received _________ ; revision accepted _________ .

Key words: arid tropical scrub; Cactaceae; fleshy-fruits; Glossophaginae; Phyllostomidae; seed germination; seedling establishment; Tehuacán Valley.

Feeding behavior of fruit-eating animals is one of the most important aspects of seed dispersal that can influence the reproductive success of plants and their population dynamics (Stiles 1992). Among the main behavioral characteristics of frugivores that determine the deposition patterns of seeds are the frequency of visits to fruiting plants, the number of seeds removed per visit, the treatment given to the seeds during gut passage, and the movement patterns which determine the potential microsites for dispersed seeds (Jordano 1992, Stiles 1992, Schupp 1993).

The fleshy-fruits of columnar cacti are consumed by a wide range of animals, including two species of nectar-feeding bats, *Leptonycteris curasoae* and *Choeronycteris mexicana* (Phyllostomidae, Glossophaginae) (Sosa & Soriano 1993, Valiente-Banuet *et al.* 1996, Petit 1997), and several species of birds (Wendelken & Martin 1988, Silvius 1995, Valiente-Banuet *et al.* 1996). Birds remove some seeds during the day and bats remove > 50% of the seeds at night (Fleming & Sosa 1994). Because the successful recruitment of many columnar cacti depends on seed germination beneath the canopies of perennial nurse plants (Turner *et al.* 1966, Valiente-Banuet & Ezcurra 1991), it is important to determine whether the behavior of frugivorous animals might result in the dispersal of seeds to sites favorable for germination and seedling establishment.

During the consumption of nectar and pollen of *Agave palmeri*, the lesser long-nosed bat (*L. curasoae*) fed in a series of discontinuous bouts alternating with resting periods spent on rocks and plants such as ocotillo (*Fouquieria splendens*), columnar cacti and paloverde (*Cercidium microphyllum*) (Howell 1979). If these bats exhibit the same foraging pattern when they visit plants for fruit, they might disperse seeds to a variety of habitats, including suitable sites for seedling recruitment. Seed dispersal by bats could occur in two different ways depending on seed size: 1) bats could swallow small seeds and pass them through their digestive tracts or 2) they could drop large seeds some distance away from parent plants after consuming the pulp (Izhaki *et al.* 1995).

In the Tehuacán Valley in south-central Mexico, a semiarid region with a high diversity of columnar cacti and phyllostomid bats (Valiente-Banuet *et al.* 1996), *L. curasoae* and *C. mexicana* consume the nocturnal-dehiscent fruits of about 14 species of columnar cacti (A. Rojas-Martínez pers. comm.). One of these species is *Neobuxbaumia tetetzo*, an 8 m tall endemic columnar cactus occurring at densities of up to 1200 individuals per hectare (Valiente-Banuet & Ezcurra 1991). Its fruits are green and are borne on the tips of branches; when ripe they dehisce at night, exposing a sugary whitish pulp with 933 ± 51 (x ± SE; $N = 35$) small black seeds. Fruit color and odor are similar to that of their flowers, which are pollinated by bats (Valiente-Banuet *et al.* 1996). These characteristics strongly suggest that seeds are bat-dispersed. In this paper, we report the results of flight cage experiments on the feeding behavior of *L. curasoae* and *C. mexicana*. The purpose of this study was to evaluate the possible effects of foraging behavior of these two bat species on dispersal of seeds of *N. tetetzo*. Specifically, we determined the frequency of visits to ripe fruits, the duration of feeding and resting periods, and the mode of fruit consumption (*i. e.*, whether seeds pass through the digestive tract or are dropped). If bats drop seeds while feeding or flying, they could disperse seeds to a wide variety of sites, including suitable germination sites beneath the canopies of trees and shrubs used as feeding roosts. In contrast, if they pass seeds through their digestive tracts, seed dispersal will depend on gut passage time, its effect on seed germination, and the place where defecation takes place.

The study was conducted in the Zapotitlán Valley (18° 20'N, 97° 28'W), a local basin of the Tehuacán Valley in the state of Puebla, Mexico. This region receives an average annual rainfall of 380 mm and has an annual mean temperature of 21°C (range 17.1-24.3°C). The main vegetation types and diversity of bats in the region have been described elsewhere (Osorio *et al.* 1996; Rojas-Martínez & Valiente-Banuet 1996).

Bats were captured with three mist nets (12 m x 3 m) placed in patches of *Neobuxbaumia tetetzo* and opened from about 2000 to 2300 h. Individuals were identified to species, and non-reproductive adults of both sexes were used. Bats were placed in cloth bags for approximately 1 h before experiments were conducted.

One branch of *N. tetetzo* with five mature fruits was collected in the field. This branch was placed inside a flight cage (5 m x 4 m x 3 m) in which bats were released and allowed to feed approximately 1 h after capture. We observed bats inside the cage with dim light. A single bat was used in each trial. We recorded the timing and frequency of visits to each fruit. A visit was defined as a flight of a bat to the fruits in which a portion of the fruit pulp was removed. The duration of feeding and resting periods was determined based on the criteria used by Bonaccorso & Gush (1987). According to this, a feeding period consisted of a series of visits to fruits in which the time elapsed between visits was < 10 min. An interval of > 10 min between visits was considered a resting period.

The duration of feeding experiments ranged from 90 to 130 min per bat. No bats were kept for more than one night; bats that were not active after 1 h of their introduction into the flight cage were released. Fruits offered to the bats that were completely depleted during the feeding experiment were replaced with new ones.

We observed the feeding behavior of five individuals of *L. curasoae* and three of *C. mexicana* for a total of 9.5 h and 4.3 h, respectively. Both species exhibited similar behavior which consisted of short feeding periods alternating with longer resting periods (Table 1). This behavior is similar to that reported by Bonaccorso & Gush (1987) for other phyllostomid species such as *Carollia perspicillata* and *C. subrufa*. Howell (1979) reported that the foraging pattern of *L. curasoae* at *Agave palmeri* flowers included feeding and resting periods of 20 min each (but see Horner *et al.* 1998 for different results).

Bat behavior during feeding periods involved flights around the cage to select a fruit for consumption. This flight lasted a few seconds, and when a fruit was selected, the bat bit a part of it while in flight. Once a piece of fruit was removed, bats flew for a few seconds around the cage and then landed on a particular place on the ceiling where they consumed only the pulp and spit out the majority of seeds. Many seeds were also dropped to the ground while the bats handled the piece of fruit on the perch. The mean number of seeds ± SE found per feces for both bat species was 40.8 ± 56.4 (*N* = 6; range 2-145), whereas the mean number of seeds per fruit was 933 ± 51 (*N* = 35). Consequently, the proportion of seeds passing through the digestive tract per fecal sample was 4.4%. Considering the low proportion of seeds per fecal sample in comparison with the seeds that were spit out or dropped by bats, we assume that few seeds pass through the digestive tract of bats during dispersal. Morrison (1980) studied the food utilization efficiency of *Artibeus jamaicensis* (Phyllostomidae, Stenodermatinae) and estimated that this species swallowed about 80% of the 160 ± 37 seeds per fig. *L. curasoae* and *C. mexicana* made several visits to a fruit before its pulp was depleted. The mean number of visits per hour ± SE for *L. curasoae* was 17.9 ± 4.0 ($N = 5$; range 8.4-28.9), and for *C. mexicana* it was 20.7 ± 6.4 ($N = 3$; range 14.3-27.1). Bizerril & Raw (1998) studied the feeding behavior of *Carollia perspicillata* and *Glossophaga soricina* under natural conditions and found that the mean number of visits per hour for both species was 14.2 ± 8.4.

During resting periods, bats groomed themselves and slept. This behavior was recorded in all individuals of both species and comprised about 75% of their total activities (Table 1). Time schedule for three individuals of *L. curasoae* and *C. mexicana* with their frequency of visits to fruits and the duration of feeding and resting periods are shown in Fig. 1.

Our observations on the feeding behavior of *L. curasoae* and *C. mexicana* suggest that they are dispersers that transport seeds away from fruiting plants before dropping them beneath perches. Fleming & Sosa (1994) reported that bats of the genus *Leptonycteris* remove 10-80% of the available seeds of the cactus *Pachycereus pringlei* each night. Because these bats consume fruit pulp while perched and spit out the majority of seeds, they could deposit large numbers of seeds in a variety of habitats including plants, rocks and rock crevices (Hirshfeld *et al.* 1977). Trees and shrubs most commonly used as night-roosts by bats of American deserts include ocotillo (*Fouquieria splendens*), paloverde (*Cercidium microphyllum*), blackbrush (*Coleogyne ramosisima*), creosote bush (*Larrea tridentata*), four-winged saltbush (*Atriplex canescens*) and columnar cacti (Hirshfeld *et al.* 1977, Howell 1979). In tropical forests, Bonaccorso & Humphrey (1984) reported that this behavior promotes the regeneration of colonizing plants such as *Piper*, which depend on forest gaps for their establishment. However, Fleming (1981) found that the bat *Carollia perspicillata* deposits many seeds of this plant in unsuitable germination sites. In the Tehuacán Valley, night-roosts used by *L. curasoae* and *C. mexicana* include the dominant species of shrubs, *Mimosa luisana*, *Caesalpinia melanadenia*, *Cercidium praecox*, and the columnar cacti *Neobuxbaumia tetetzo* and *Stenocereus stellatus* (A. Rojas-Martínez pers. comm.). Some of these plants have significantly higher numbers of young individuals of *N. tetetzo* growing beneath their canopies than expected by chance (Valiente-Banuet *et al.* 1991).

In conclusion, our observations of the behavior of *L. curasoae* and *C. mexicana* when feeding on *N. tetetzo* fruits indicate that these bats drop many seeds beneath their feeding-roosts. Considering that these roosts in nature include trees and shrubs, bat-feeding behavior may promote seedling recruitment in *N. tetetzo*.

We thank Antonio Soriano and Rodolfo Reséndiz for their assistance during field work and experimental trials. We also thank Alberto Rojas Martínez who provided information on bat roosts in the Tehuacán Valley. Theodore H. Fleming and Jay F. Storz provided critical reviews of the manuscript. This study was supported by Fondo Mexicano para la Conservación de la Naturaleza A-1-97/36 and Dirección General de Asuntos del Personal Académico IN-207798.

Bizerril, M. X. A., and A. Raw. 1998. Feeding behaviour of bats and the dispersal of *Piper arboreum* seeds in Brazil. J. Trop. Ecol. 14: 109-114.

Bonaccorso, F. J., and S. R. Humphrey. 1984. Fruit bat niche dynamics: their role in maintaining tropical forest diversity. *In* A. C. Chadwick and S. L. Sutton (Eds.). Tropical rain-forest. The Leeds Symposium, pp. 169-183. Leeds Philosophical and Literary Society, U. K.

---------, and T. J. Gush. 1987. Feeding behaviour and foraging strategies of captive phyllostomid fruit bats: An experimental study. J. Anim. Ecol. 56: 907-920.

Fleming, T. H. 1981. Fecundity, fruiting pattern, and seed dispersal in *Piper amalago* (Piperaceae), a bat-dispersed tropical shrub. Oecologia (Berl.) 51:42-46.

Fleming, T. H., and V. J. Sosa. 1994. Effects of nectarivorous and frugivorous mammals on reproductive success of plants. J. Mammal. 75: 845-851.

Hirshfeld, J. R., Z. C. Nelson, and G. Bradley. 1977. Night roosting behaviour in four species of desert bats. Southwest. Nat. 22: 427-433.

Horner, M. A., T. H. Fleming, and C. T. Sahley. 1998. Foraging behaviour and energetics of a nectar-feeding bat, *Leptonycteris curasoae* (Chiroptera: Phyllostomidae). J. Zool., Lond. 244: 575-586.

Howell, D. J. 1979. Flock foraging in nectar-feeding bats: Advantages to the bats and to the host plants. Am. Nat. 114: 23-49.

Izhaki, I., C. Korine, and Z. Arad. 1995. The effect of bat (*Rousettus aegyptiacus*) dispersal on seed germination in eastern Mediterranean habitats. Oecologia 101: 335-342.

Jordano, P. 1992. Fruits and frugivory. *In* M. Fenner (Ed.). Seeds: the ecology of regeneration in plant communities, pp. 105-156. CAB International, Wallingford, UK.

Morrison, D. W. 1980. Efficiency of food utilization by fruit bats. Oecologia (Berl.) 45: 270-273.

Osorio, B. O., A. Valiente-Banuet, P. Dávila, and R. Medina. 1996. Tipos de vegetación y diversidad en el Valle de Zapotitlán de las Salinas, Puebla, Mexico. Bol. Soc. Bot. Mex. 59: 35-58.

Petit, S. 1997. The diet and reproductive schedules of *Leptonycteris curasoae curasoae* and *Glossophaga longirostris elongata* (Chiroptera: Glossophaginae) on Curaçao. Biotropica 29: 214-223.

Rojas-Martínez, A. and A. Valiente-Banuet. 1996. Análisis comparativo de la quiropterofauna del Valle de Tehuacán-Cuicatlán, Puebla-Oaxaca. Acta Zool. Mex. (n. s.) 67: 1-23.

Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio 107/108: 15-29.

Silvius, K. M. 1995. Avian consumers of cardón fruits (*Stenocereus griseus*: Cactaceae) on Margarita Island, Venezuela. Biotropica 27: 96-105.

Sosa, M., and P. J. Soriano. 1993. Solapamiento de dieta entre *Leptonycteris curasoae* y *Glossophaga longirostris* (Mammalia: Chiroptera). Rev. Biol. Trop. 41: 529-532.

Stiles, E. W. 1992. Animals as seed dispersers. *In* M. Fenner (Ed.). Seeds: the ecology of regeneration in plant communities, pp. 87-104. CAB International, Wallingford, UK.

Turner, R. M., S. M. Alcorn, G. Olin, and J. A. Booth. 1966. The influence of shade, soil and water on saguaro seedling establishment. Bot. Gaz. 127: 95-102.

Valiente-Banuet, A., and E. Ezcurra. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse-plant *Mimosa luisana* in the Tehuacán Valley, Mexico. J. Ecol. 79: 961-971.

---------, A. Bolongaro-Crevenna, O. Briones, E. Ezcurra, M. Rosas, H. Núñez, H. Barnard, and E. Vázquez. 1991. Spatial relationships between cacti and nurse shrubs in a semi-arid environment in central Mexico. J. Veg. Sci. 2: 15-20.

---------, M. del C. Arizmendi, A. Rojas-Martínez, and L. Domínguez-Canseco. 1996. Ecological relationships between columnar cacti and nectar-feeding bats in Mexico. J. Trop. Ecol. 12: 103-119.

Wendelken, P. W. and R. F. Martin. 1988. Avian consumption of the fruit of the cacti *Stenocereus eichlamii* and *Pilosocereus maxonii* in Guatemala. Am. Midl. Nat. 119: 235-243.

Héctor Godínez-Alvarez and Alfonso Valiente-Banuet

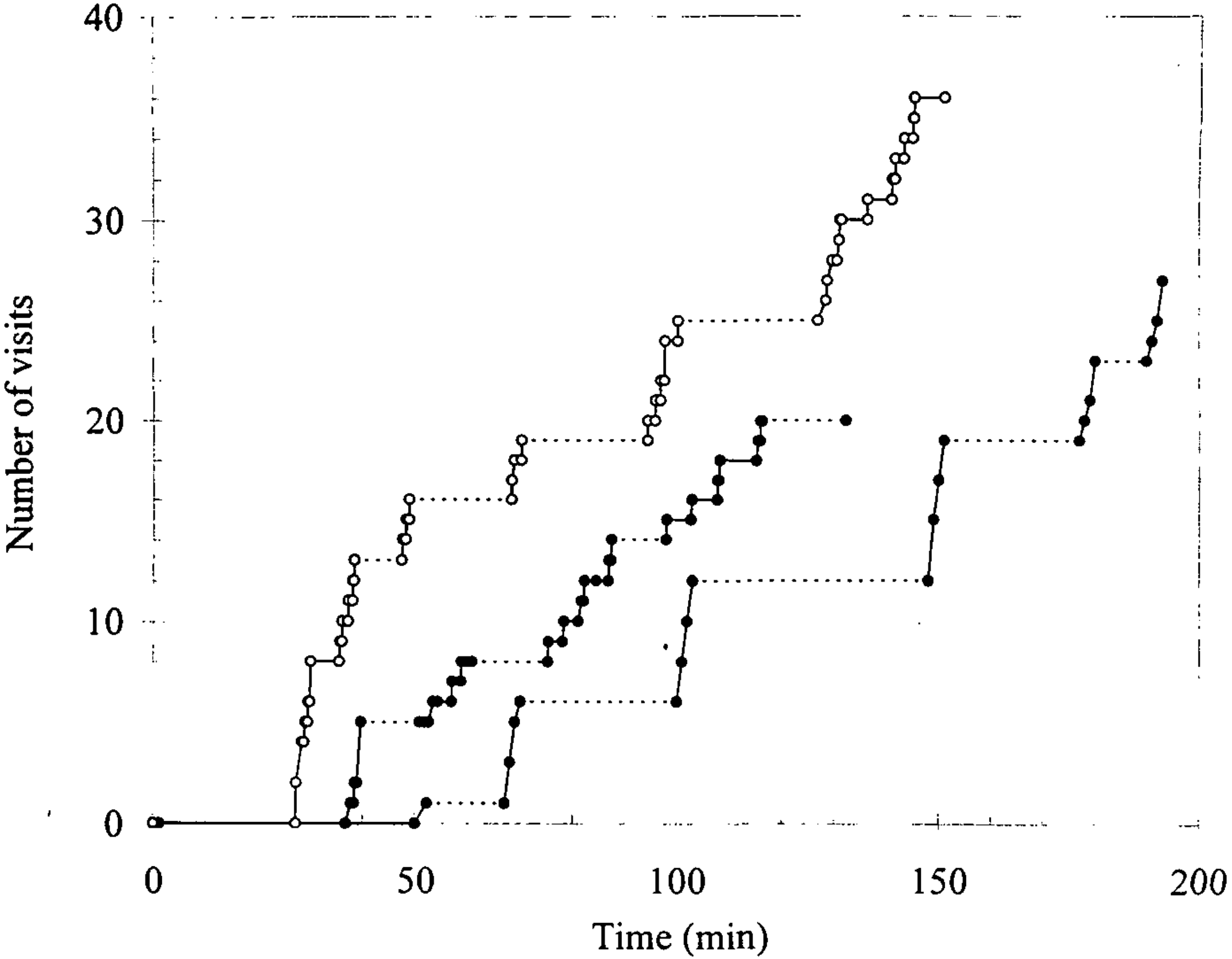
Instituto de Ecologia, Universidad Nacional Autónoma de México. Apartado Postal 70-275, Coyoacán C. P. 04510. México, D.F.

TABLE 1. Duration of feeding and resting periods (min) and proportion of time spent resting for *L. curasoae* and *C. mexicana* bats while feeding on *N. tetetzo* fruits in flight cage experiments. Values are mean ± SE.

Bat species	*N*	Feeding period	Resting period	% Time resting
Leptonycteris curasoae	5	7.4 ± 5.4	20.3 ± 12.2	71.7 ± 4.8
Choeronycteris mexicana	3	6.4 ± 7.3	17.2 ± 6.7	73.8 ± 5.3

Figure Legend

FIGURE 1. Number of visits by three individuals of *Leptonycteris curasoae* (closed circles) and *Choeronycteris mexicana* (open circles) to fruits of *Neobuxbaumia tetetzo*. showing feeding (continous lines) and resting periods (dotted lines).


40
30
20
10
0
Number of visits
0
50
100
150
200
Time (min)

Running head: Seed dispersal and *N. tetetzo* population dynamics

The role of seed dispersers in the population dynamics of the columnar cactus *Neobuxbaumia tetetzo*

Héctor Godínez-Alvarez, Alfonso Valiente-Banuet and Alberto Rojas-Martínez

Instituto de Ecología, Universidad Nacional Autónoma de México
Apartado Postal 70-275, Coyoacán, C. P. 04510
México, D. F.

ABSTRACT

We examined the effect of frugivorous bats and birds on the population dynamics of the giant-columnar cactus *Neobuxbaumia tetetzo* in the Tehuacán Valley. Because successful seedling establishment occurs only beneath the canopies of shrubs and trees, we hypothesized that directed seed dispersal, which allows the removal of seeds to these sites, is a key process in the maintenance of its populations. We determined the dispersal effectiveness of different frugivores, considering the quantity and quality components of seed dispersal. We evaluated the potential effects of each frugivore species on the finite rate of increase of *N. tetetzo* populations by modifying the fecundity values of a Lefkovitch matrix model. The bat *Leptonycteris curasoae* had the highest effectiveness whereas the birds *Zenaida asiatica* and *Carpodacus mexicanus* had the lowest. The quality component of dispersal was more important than the quantity one to determine dispersal effectiveness. The estimated finite rates of increase calculated to evaluate the effects of frugivores on the population dynamics of the cactus were not significantly different from unity, except when the effect of the seed predator *Carpodacus mexicanus* was analyzed. Our results suggest that the bat *Leptonycteris curasoae* could be considered the legitimate dispersal agent of *N. tetetzo*, which directly disperse seeds to safe sites, representing a key species in the ecology of this columnar cactus.

Key words: arid tropical scrub; bats; birds; finite rate of increase; frugivory; *Leptonycteris curasoae*; matrix models; safe sites; seed dispersal; seed germination; seedling establishment; Tehuacán Valley.

Key phrases: Columnar cacti ecology; Directed seed dispersal to safe sites; Effects on population dynamics; Fruit-eating birds and mammals; Keystone species in community diversity; Quantity vs. Quality; Seed dispersal effectiveness; Seed dispersers vs. Seed predators.

INTRODUCTION

In deserts the successful establishment of columnar cacti occurs only in safe sites beneath the canopies of perennial nurse plants which ameliorate environmental conditions, enhancing seed germination and seedling survivorship (Shreve 1931, Turner et al. 1966, Steenbergh and Lowe 1969, Valiente-Banuet and Ezcurra 1991). We assume that seed dispersal may considerably affect the population dynamics of cacti, since the survival of those stages associated to trees and shrubs has been reported to be the most important life-history parameter affecting the finite rate of increase of *Neobuxbaumia tetetzo* (Coulter) Backeberg populations (Godínez-Alvarez et al. 1999), as well as other columnar cacti populations such as *Carnegiea gigantea* (Engelm.) Britt. & Rose (Steenbergh and Lowe 1969, 1977) and *Pachycereus pringlei* (S. Watson) Britton & Rose (C. Silva-Pereyra, unpublished manuscript). Animal vectors that disperse seeds in these environments might be playing a key role in the maintenance of plant populations, because they act as the link between plant reproduction and the subsequent recruitment of new individuals established under the canopies of nurse plants (Valiente-Banuet et al. 1991, Herrera et al. 1994, Godínez-Alvarez et al. 1999). Particularly, the physiology and activities of frugivores might play an outstanding role in this respect, because they determine the moment, the site and the conditions in which seeds are deposited (Jordano 1992, Schupp 1993, Loiselle and Blake 1999).

The contribution of frugivores to the demography of the dispersed plants depends on both the quantity of seeds dispersed and the quality of the dispersal provided to each seed (Schupp 1993). The independent evaluation of these two components of seed dispersal is ecologically important because it allows the identification of the legitimate dispersal agents for particular plant species. Often frugivores that disperse the majority of seeds do not always provide the best quality of dispersal; and in contrast, frugivores that provide the best quality of dispersal are not necessarily those that disperse the highest number of seeds (Reid 1989, Schupp 1993, Loiselle and Blake 1999). The product of these two components determine the dispersal effectiveness (sensu Schupp 1993), indicating whether a particular animal species is a legitimate dispersal agent for a certain plant species or it behaves rather as a seed predator.

Several works have estimated the dispersal effectiveness of different species of fruit-eating animals using different approaches to analyze the quantity and quality components of seed dispersal (Reid 1989, Chavez-Ramirez and Slack 1994, Sun et al. 1997, Loiselle and Blake 1999). Despite this information is essential to understand the importance of one or various frugivores in relation to the quantity or quality of dispersed seeds; at present, the determination of the actual contribution of seed dispersers to plant population dynamics is the primary goal in the study of seed dispersal. In order to accomplish this goal it is necessary to estimate not only the quantity and quality components of effectiveness, but also the survival and growth probabilities of the dispersed seeds and the subsequent stages such as seedlings, saplings and adults (Loiselle and Blake 1999). One approach towards this general understanding of the role of seed dispersers in the population dynamics of plants is to combine the assessment of the effectiveness of each disperser with a demographic model in which to integrate the quantity and quality components of seed dispersal in the fecundity values of reproductive size categories and to determine their effect on the finite rate of increase.

Within the tropics and in the rain-shadowed deserts located in south-central Mexico, columnar cacti are the physiognomic and structural dominant elements of different vegetation types called "columnar cactus forests" (Valiente-Banuet et al. 1996). In these ecosystems a total of 34 species of bats and 91 species of birds have been reported (Arizmendi and Espinosa de los Monteros 1996, Rojas-Martinez and Valiente-Banuet 1996); some of these animals, maintain tight and coupled biotic interactions with columnar cacti (Valiente-Banuet et al. 1996, 1997a,b). *Neobuxbaumia tetetzo* is an 8 m tall branched columnar cactus which dominates the vegetation over ca. 400 km^2 in the Tehuacán-Cuicatlán Valley, whose fruits are consumed by nine species of bats and birds (Valiente-Banuet et al. 1996). In this study, we address some questions that aim to determine (1) what is the effectiveness of the different seed dispersal agents of *N. tetetzo*?, and (2) what are their relative impact on the population dynamics of this columnar cactus in the Tehuacán Valley, Mexico?. Our primary goal was to determine the dispersal effectiveness of different frugivorous species, considering both the quantity and the quality components proposed by Schupp (1993). We also determined the average number of seeds removed from *N. tetetzo* fruits by birds and bats, the main frugivore groups. Finally, we incorporated all this information into a population projection matrix model for *N. tetetzo* to analyze the effects of animal vectors on its population finite rate of increase.

STUDY SITE AND METHODS

This study was conducted in the semiarid Valley of Zapotitlán (18°20'N, 97°28'W), a local basin of the Tehuacán Valley in the state of Puebla, Mexico. This region owes its aridity to the rain shadow produced by the Eastern Sierra Madre (Smith 1965). It has an annual average rainfall of 380 mm, most of which falls during the summer months, and an annual mean temperature of 21°C with rare frosts (García 1973). The area is heterogeneous with hills and mountains dominating the landscape. Flat areas occur only on alluvial deposits along Río Salado. Different lithologies are present in the study area including shale, limestone and igneous materials (Brunet 1967). The main vegetation types, edaphically controlled, are characterized by the dominance of columnar cacti reaching densities of 1800 individuals/ha (Osorio et al. 1996). The study was conducted in an area near Cerro Cutá, within the land of the "Helia Bravo" Botanical Garden, located approximately 30 km south of Tehuacán city in which *Neobuxbaumia tetetzo* dominates with densities of ca. 1200 individuals/ha (Valiente-Banuet and Ezcurra 1991). Seed germination and seedling establishment occurs mostly beneath the canopies of the legumes *Mimosa luisana* Brandegee, *Caesalpinia melanadenia* (Rose) Standley and *Senna wislizenii* (A. Gray) Irwin & Barneby, producing an association of the species to these shrubs (Valiente-Banuet et al. 1991). Flowering and fruiting seasons occur from mid-April until the end of June, just before the rainy season. The species is hermaphroditic and its flowers are whitish and mainly nocturnal, opening at dusk (2000 h) and closing in the early morning (0600 h). The bats *Choeronycteris mexicana* Tschudi and *Leptonycteris curasoae* Miller are the only pollinators that promote seed production (Valiente-Banuet et al. 1996). Fruits are green and grow on the tips of branches; they are 35.5 ± 4.3 mm long (mean ± S. D.; n = 39), 25.0 ± 1.9 mm wide (n = 39) and weigh 11.5 ± 1.8 g (n = 39). Ripe fruits dehisce at night, exposing a sugary whitish pulp with an average of 933 ± 302 (n = 35) small black seeds. Fruit color and odor very similar to the flowers correspond to a bat-dispersal syndrome (van der Pijl 1982).

Effectiveness of seed dispersal

Dispersal effectiveness was estimated considering aspects of the quantity and quality components of seed dispersal proposed by Schupp (1993). As detailed below, the quantity component was estimated using data on the relative abundance of frugivores and the frequency of visits to the fruits per hour. The quality component was estimated using data on seed germination after gut passage and the probability of seeds being deposited under shrub and tree canopies (i. e. safe sites; Valiente-Banuet and Ezcurra 1991). Effectiveness of each frugivore species was calculated as the product of the four components (Effectiveness = relative abundance x frequency of visits x seed germination x deposition probability under shrubs). Because the fruits of *N. tetetzo* are eaten during both the day and the night, we used different methods to estimate the components of effectiveness for birds and bats. The methods employed were selected considering the biology of both groups of frugivores. As will be noticed below, these methodological differences have direct consequences on the value of effectiveness, and therefore on the comparison of effectiveness among the different species of birds and bats. However, we considered that each method provides useful and real information on which to base our calculations; thus we used them in order to obtain estimates of the four components of dispersal effectiveness for both groups of frugivores.

Quantity component

Relative abundance of birds was estimated using the point count method (Hutto et al. 1986b). We selected six census points within an area of ca. 2 ha at the Botanical Garden, that were at least 200 m apart. In each census point all birds seen or heard during a 10 min period within a 25 m radius from the census point were recorded and identified to species. Birds detected beyond the 25 m radius during censuses were also recorded. Censuses were made daily in the morning (0700 to 0830 h) from May 10 to June 30, for a total of 15 h. The frequency of visits to *N. tetetzo* fruits was determined through daily observations of a group of 3-5 reproductive individuals from a distance of approx. 30 m. Observations were made in the morning (0700 h to 1400 h) and in the afternoon (1500 h to 1900 h) in periods of 15 minutes to record visitor species, frequency and duration of visits. These observations were made from May 15 to June 15, for a total of 70 h. Bird abundances were standardized and calculated as the number of birds per hour.

Relative abundance of bats was determined using data gathered from 1993 to 1996. During this period three mist-nets (20 m x 3 m) were placed monthly in patches of *N. tetetzo* from April to June, the reproductive season of this columnar cactus. Nets were located near fruiting plants from 1900 h to 0600 h for two consecutive nights. The total netting-effort for the years sampled was 1543 h. Bat abundance was standardized to the number of individuals per hour, per net. The frequency of bat visits to the fruits of *N. tetetzo* was determined by observations made in captivity of five individuals of *Leptonycteris curasoae* and three of *Choeronycteris mexicana*. These bats were captured from May 30 to June 7 with three mist nets (12 m x 3 m) placed in patches of *N. tetetzo* from 2000 to 2300 h. Animals were released inside a flight cage (5 m x 4 m x 3 m) in which there was a branch of *N. tetetzo* with ripe fruits. Bats were observed with dim light to record the frequency of visits to fruits and the proportion of time spent feeding and resting. The proportion of time spent resting was used to estimate the probability of deposition of seeds by bats as detailed below. One bat was used in each trial. A visit was defined as a flight event in which a portion of the fruit pulp was removed by the bat.

Additional observations were made in our study site to determine whether there were other animals, in addition to birds and bats, that fed on *N. tetetzo* fruits.

Quality component

The effect of gut passage on seeds was estimated through germination experiments to determine the proportion of germinated seeds and their germination rate. In these experiments seeds defecated by different species of birds and bats were used. The animals were captured with three mist-nets (20 m x 3 m) placed in a *N. tetetzo* patch during day (0700 h to 1100 h) and night (2000 h to 2300 h) from May through June 1997. Captured individuals were placed in cages (60 cm x 30 cm x 40 cm) for 2-3 h and fed with *N. tetetzo* fruits offered *ad libitum*. During this period birds and bats were maintained in a separate room and care was taken to avoid disturbing them as far as possible. After this time, animals were released and their feces were collected.

Defecated seeds from other animals such as coyote (*Canis latrans* Say) and gray-fox (*Urocyon cinereoargenteus* Schreber) were obtained directly from feces found in the field. These feces were collected and stored in paper bags for 1-2 days until the experiments were conducted.

Seeds obtained from feces of each animal species were sown in Petri dishes with filter paper (Whatman No. 1) moistened with distilled water. Germination took place at room temperature and natural day-light conditions. Dishes were checked daily to record the number of germinated seeds. The criterion used to consider a seed germinated was radicle emergence. The number of seeds sown per dish varied between 25-50, depending on the defecated seeds available per species; four dishes per species were sown. The proportion of germinated seeds after 7-10 days in these experimental trials was compared against a control treatment in which seeds were extracted directly from fruits and sown in Petri dishes. Results were analyzed with a log-linear model adjusted with binomial errors and multiple comparison t-tests were used to determine differences in the effect of seed passage through the gut of different animal species. The analysis was performed using the GLIM statistical package version 3.77 (Crawley 1993). The null hypothesis considered an equal proportion of germinated seeds between the treatments and the control.

Germination rates and 95% confidence limits for each species were estimated with logistic regressions using non-linear functions of the SYSTAT program version 5.0. The logistic regression is commonly used to describe data on proportions as follows:

$$y = \frac{e^{a+bt}}{1 + e^{a+bt}} * k$$

where y is the number of germinated seeds at time t, a is intercept at $t = 0$, b is the germination rate and k is the maximum number of germinated seeds.

The probability of depositing seeds under nurse canopies was estimated by focal observations to describe bird landing behavior after fruit consumption. A group of 3-5 *N. tetetzo* plants with ripe fruits was selected and observations were made daily through binoculars from a distance of about 50-100 m. The number of visits to each landing plant species per bird was recorded and grouped into three distinct categories: 1) visits to *N. tetetzo*: birds spent most of the time on the tips of the columnar cactus branches, 2) visits to trees and shrubs: birds spent most of the time among branches of different woody plants and, 3) visits to other non-shruby plants: birds spent most of the time in plants such as agaves and prickly pears. Focal observations ended when animals could not be followed or went out of the observation field. Observations were made for 20 consecutive days, starting at 0700 h and ending at 1900 h. Total observation time was 50 h and, after this time, presumably all potentially landing plant species were detected

(Fig. 1). A contingency table was used to analyze if there were significant differences in the frequency of each category of landing plants among the different bird species recorded. The null hypothesis considered an equal number of visits between categories. The probability that seeds would be deposited in safe sites was determined per bird species estimating the proportion of visits to a particular landing plant category (i. e. *N. tetetzo*, shrubs or other non-shruby plants) with respect to the total number of visits recorded.

The probability of seed deposition by the bats *Leptonycteris curasoae* and *Choeronycteris mexicana* was estimated using the methodology previously described to estimate the frequency of visits to *N. tetetzo* fruits. This deposition probability was calculated as the proportion of time that bats spent resting. Considering that in the Tehuacán Valley the night-roosts used by these bat species include dominant trees and shrubs (Godínez-Alvarez and Valiente-Banuet in press), the proportion of time spent resting could be taken as a rough estimate of the probability that bats deposit seeds in safe sites.

Seed removal by birds and bats

A fruit removal experiment was conducted in the field from May through June 1997 to estimate the average number of seeds removed by birds and bats. Each day all of the available ripe dehiscent fruits from at least 10 different plants were tagged and assigned randomly to one of the following treatments each night: 1) bird removal: fruits were bagged with nylon mesh during the night and exposed to birds from 0700 to 1800 h, and 2) bat removal: fruits were covered during the day and exposed to bats during the night from 1900 to 0600 h. Because *N. tetetzo* fruits ripe gradually along the reproductive season, the number of fruits used per treatment varied according to the number of fruits available per night. For each treatment the proportion of pulp and seeds removed per fruit was estimated considering four distinct categories: 1) consumption of less than 25% of the fruit; 2) consumption of 25-50% of fruit; 3) consumption of 50-75% of fruit; 4) consumption of more than 75% of the fruit. A fruit was considered eaten when a portion of its pulp and seeds was absent and no evidence could be found that it had fallen down to the ground around plants by mechanical action. All fruits used each night were removed from the plants. Data were analyzed with a contingency table to determine if the proportion of pulp and seeds removed differed significantly between the bird and the bat groups. The null hypothesis considered that there were no significant differences between birds and bats in the proportion of pulp and seeds they removed. The proportion of seeds removed by each group of frugivores was multiplied by the mean number of seeds per fruit to estimate the number of seeds removed by each group.

Effect of seed dispersal on *N. tetetzo* population dynamics

The effect of seed dispersal on the finite rate of increase of *N. tetetzo* populations was estimated using a Lefkovitch matrix model previously built for this population at this study site (Table 1; Godínez-Alvarez et al. 1999). In this demographic model, individuals were grouped in size categories and a one-year projection matrix was constructed according to the survival, reproduction and growth probabilities of the individuals in each category. The size categories used in this matrix were: 0-2 cm, seedling 1; 2-8 cm, seedling 2; 8-15 cm, seedling 3; 15-45 cm, sapling; 45-100 cm, juvenile; 100-150 cm, immature; 150-250 cm, mature 1; 250-350 cm, mature 2; 350-450 cm, mature 3; 450-550 cm, mature 4; 550-650 cm, mature 5; >650 cm, mature 6. This matrix is conformed of three main parts: (1) The first row includes the fecundity values for all the reproductive classes. These fecundity values were estimated as the product of the probability of reproduction, the mean number of seeds produced by an average individual of each reproductive class, the probability of passing from seed to seedling which was calculated assuming a random dispersion of seeds and considering the proportions of soil covered by shrubs and deprived of vegetation as well as the number of survivors in open spaces and beneath shrubs, and the probability that a seedling grows to the seedling 1 category. (2) The main diagonal includes the probabilities that individuals remain in the same size class after one year. (3) The first lower sub-diagonal incorporates the probabilities that individuals grow to the next size class after one year. The finite rate of increase of the *N. tetetzo* population estimated by this model was 1.0 with 90% confidence limits of 0.94 and 1.01 (Godínez-Alvarez et al. 1999).

We incorporated the effect of seed dispersal by each animal vector into the matrix model by modifying the fecundity values according to our estimate of the "effect of seed dispersal" for each frugivore species. This "effect of seed dispersal" was a product of a) the probability of seed removal by each disperser species; b) the proportion of germinated seeds after gut passage; c) the probability that the disperser would deposit the seeds beneath the canopy of a nurse plant; and d) the survival probability of seeds beneath shrubs (0.00139). In turn, the calculation of a), the probability of seed removal, was a function of several measures: first, we multiplied the relative abundance of each disperser species by its frequency of visits to *N. tetetzo* fruits; then, the result was multiplied by the average number of seeds removed by the relevant group (i. e., 233 seeds removed, on average, by birds; and 700 by bats –see results below); finally, these data were added up across all disperser species. Of this total, the relative proportion corresponding to each disperser species was interpreted as the probability of seed removal per species.

Once the "effect of seed dispersal" was calculated as detailed above for each disperser species, it was incorporated in the matrix model by substituting it as the "probability of passing from seed to seedling" in the calculation of fecundity values detailed above.

Three types of matrix simulations were performed to estimate the finite rate of increase of the *N. tetetzo* population considering: 1) the effect of all dispersers acting together, 2) the individual effect of each disperser, and 3) the effect of the seed predator *Carpodacus mexicanus* P. L. S. Muller. To simulate the effects of all disperser species acting together we calculated the probability of seed removal as the sum of all the probabilities estimated for each species whereas the germination proportion after gut passage and the deposition probability were estimated as the mean weighted by the seed removal probability.

For each simulation we estimated the finite rate of increase using the program STAGECOACH ver. 2.3 (Cochran and Ellner 1992), and its 90% confidence limits to determine whether it differed from unity (i. e. whether the population may be considered in a numerical equilibrium). Confidence limits for λ were obtained using Monte Carlo simulation models in which the variances for matrix entries were estimated assuming a log-normal distribution of errors for fecundity values and a multinomial distribution of errors for transition probabilities (Alvarez-Buylla and Slatkin 1993). With these assumptions, 1000 simulations were conducted and the sampling distribution of lambda was constructed for each matrix. Confidence limits were determined considering the values of the 5 and 95 percentiles.

RESULTS

Effectiveness of seed dispersal

Quantity component

Eleven species of birds such as the white-winged dove (*Zenaida asiatica* Linnaeus), the northern mockingbird (*Mimus polyglottos* Linnaeus) and the house finch (*Carpodacus mexicanus*), among others visited the fruits of *N. tetetzo* (Table 2). All observed species fed only on fruits whereas *C. mexicanus* and *Melanerpes hypopolius* Wagler also fed on flowers. *Z. asiatica* and *C. mexicanus* were the species with the highest relative abundance followed by *M. polyglottos*, *Campylorhynchus brunneicapillus* Lafresnaye, *Melanerpes hypopolius* and *Aimophila mystacalis* Hartlaub (Table 2).

Z. asiatica and *C. mexicanus* were the most frequent visitors to *N. tetetzo* fruits. Their visits added up to more than 70% of the total number of visits recorded for birds and their frequency of visits were over one visit per hour. In contrast, the visits of the rest of the species were less than 10% of the total number of visits and their frequency of visits was lower than one visit per hour (Table 3). The number of visits to *N. tetetzo* fruits varied throughout the day, showing two peaks of activity: the first peak was observed in the morning around 0930 h, whereas the second occurred in the afternoon at approximately 1730 h. Bird activity decreased at noon between 1200 h and 1600 h (Fig. 2).

The main bats that consumed *N. tetetzo* fruits were the phyllostomids *Leptonycteris curasoae*, *Choeronycteris mexicana* and *Artibeus jamaicensis* Leach. Of these species, *L. curasoae* and *C. mexicana* had the highest relative abundance (Table 2). The mean frequency of visits per hour ± S. E. for *L. curasoae* was 17.9 ± 4.0 (n = 5) whereas for *C.*

mexicana it was 20.7 ± 6.4 (n = 3). The frequency of visits for *A. jamaicensis* could not be estimated since during the field work we did not capture any individual of this species.

Besides birds and bats, the coyote (*Canis latrans*) and the gray-fox (*Urocyon cinereoargenteus*) also fed on the fruits of *N. tetetzo* once they fell to the ground.

Quality component

The effect of gut passage on the proportion of germinated seeds and their germination rate was estimated only for five species of birds and three species of mammals (Table 4). Seeds defecated by the birds *C. brunneicapillus*, *Toxostoma curvirostre* Swainson, *M. polyglottos* and *M. hypopolius* presented the highest germination percentages (> 95%) not differing from control seeds (99%). In contrast, germination of seeds defecated by bats (*L. curasoae*) and gray-foxes (*U. cinereoargenteus*) varied between 80% and 86% differing significantly from the control. Seeds defecated by *Canis latrans* and *A. mystacalis* had a germination lower than 50%. The birds *Z. asiatica*, *C. psaltria* and *C. mexicanus* destroyed all seeds and no germination was observed (Table 4).

The estimated germination rates for all species varied from 1.0 to 5.7 germinated seeds per day. *M. polyglottos* and *A. mystacalis* were the species with the highest and lowest rates, respectively. In spite of these differences, the 95% confidence intervals showed that there were no statistically significant differences among them (Table 4). Therefore, germination rates were not included in the estimation of dispersal effectiveness. Seed germination curves after gut passage for different mammal and bird species showed that germination was a rapid process that occurred within the first 3-5 days after sowing, depending on the frugivorous species (Fig. 3).

After fruit consumption, birds landed on different plant species including shrubs, trees and columnar cacti, among others (Table 5). The number of times that *Z. asiatica* and *M. hypopolius* landed on *N. tetetzo* plants was higher than the number of landings on other plants. In contrast, *M. polyglottos* landed on shrubs more frequently than on *N. tetetzo* ($G = 259.5$, d.f. 12, $p < 0.00001$). For the rest of the species we did not find significant differences in their number of landings on *N. tetetzo* and on shrubs compared to expected values (Table 5).

The bats *L. curasoae* and *C. mexicana* consumed only the pulp of the fruits and spit out the majority of seeds beneath their perches. The proportion of time spent resting for both species was 71.7 ± 4.8% (mean ± S. E.; $n = 5$) and 73.8 ± 5.3% ($n = 3$), respectively, thus the probability of seed deposition was 0.72 for *L. curasoae* and 0.74 for *C. mexicana*.

Of all the species of birds and mammals studied, we obtained the complete data necessary to estimate the effectiveness of dispersal only for six species of birds and one species of bat (Table 6). The dispersal effectiveness estimated for these frugivores showed that the lesser long-nosed bat (*Leptonycteris curasoae*) had the highest value given by both a high frequency of visits to fruits and a high probability of seed deposition. Other species such as the northern mockingbird (*Mimus polyglottos*), cactus wren (*Campylorhynchus brunneicapillus*), gray-breasted woodpecker (*Melanerpes hypopolius*) and curve-billed thrasher (*Toxostoma curvirostre*) presented higher relative abundance and germination percentages than bats but intermediate values of dispersal effectiveness. Although white-winged doves (*Zenaida asiatica*) and house finches (*Carpodacus mexicanus*) had the highest relative abundance, they destroy seeds either when feeding on fruits or during gut passage and thus show null dispersal effectiveness; these species act rather as seed predators (Table 6).

Seed removal by birds and bats

Bats removed a greater proportion of pulp and seeds from fruits than birds did. The number of fruits with more than 75% removal by bats were higher than expected by chance. In contrast, the number of fruits with less than 25% removal by birds were higher than expected by chance ($G = 38.6$, d.f. 3, $p < 0.0001$; Fig. 4). Considering that the mean number of seeds per fruit is 933 ± 302 (mean ± S. D.; $n = 35$), these results suggest that bats could remove an average of 700 seeds per fruit each night whereas birds may remove only an average of 233 seeds per fruit each night.

Effect of seed removal on the finite rate of increase

Table 7 shows the estimated effects of seed dispersal by each animal vector used to modify the fecundity values in the matrix model for the *N. tetetzo* population. The estimated finite rate of increase considering the effects for all dispersers acting together was 0.99 not differing significantly from unity and indicating that the population is in a numerical equilibrium (Table 7). When we considered the effects of each disperser individually, the estimated population growth rates varied among species. For instance, if only the effect of *T. curvirostre* was considered, the population of *N. tetetzo* showed a $\lambda = 0.965$, whereas if only the effect of the most effective disperser, *L. curasoae*, was included, a $\lambda = 0.989$ was obtained. The 90% confidence intervals for λ showed that the calculated finite rates of increase for the *N. tetetzo* population incorporating the individual effect of each disperser differed marginally from unity except for the lesser long-nosed bat (*L. curasoae*). On the other hand, the simulation for the seed predator *Carpodacus* *mexicanus* showed that the finite rate of increase decreased to 0.959, marginally differing from unity (Table 7).

Considering the results of this study, in figure 5 we present some of the possible paths followed by *N. tetetzo* seeds during the dispersal phase, along with their potential effects on the finite rate of increase. According to this diagram, seeds could be removed from fruits by birds and/or bats, or else they could fall down to the ground. The probability of this last event (0.03) was calculated, independently of the probability of seed removal, as the proportion of the mean number of fruits found in a 1 m^2 area (1.7 ± 0.2, mean ± S. E., n = 50) at the base of *N. tetetzo* plants with respect to the mean number of fruits per plant (49.2 ± 7.7, mean ± S. E., n = 30). Once on the ground, seeds could be highly exposed to seed predators such as the gray-foxes (*U. cinereoargenteus*), the coyotes (*C. latrans*) and the harvester ants (*Pogonomyrmex barbatus* F. R. Smith). The seeds of the fruits that remains attached to the plants could be predated by doves (*Z. asiatica*) and/or house finches (*C. mexicanus*). On the other hand, bat- and bird-dispersed seeds could be transported to safe sites beneath the canopies of trees and shrubs.

DISCUSSION

Our results indicate that *N. tetetzo* fruits are eaten by different species of birds and mammals which may disperse seeds in varying quantities and with varying degrees of dispersal quality, affecting the recruitment of new individuals. Therefore, these fruit-eating animals have a direct effect on the population dynamics of this columnar cactus.

Our analysis of dispersal effectiveness showed that the wide array of fruit-eating animals may act both as seed predators, such as *Zenaida asiatica* and *Carpodacus mexicanus*, or as seed dispersers with varying degrees of effectiveness such as *L.*

curasoae, *M. polyglottos* and *C. brunneicapillus*. These results are supported by observations made in the field as well as in captivity for different species. For example, *M. polyglottos* and *C. brunneicapillus* spent most of the time on the ground or on small perennial shrubs where they forage insects, simultaneously avoiding potential predators (Hailman 1960, Biedenweg 1983, Joern and Jackson 1983). This behavior increases the probability of depositing seeds under shrubs. On the contrary *Z. asiatica*, *C. mexicanus* and *M. hypopolius* showed a high relative abundance and frequency of visits to *N. tetetzo* fruits; however, these birds spent very little time on shrubs and, in the case of *Z. asiatica* and *C. mexicanus*, they also had a negative effect on seed germination. Despite this fact, Olin et al. (1989) found that *Z. asiatica* could accidentally disperse some viable seeds of *Carnegiea gigantea* (Engelm.) Britt. & Rose while feeding its chicks. On the other hand, *Melanerpes hypopolius* did not affect seed germination, however, this bird spent all of its time on *N. tetetzo* plants (Hendricks et al. 1990), suggesting that this species is not a good disperser.

These results suggest that, in the case of *N. tetetzo*, the quality component of seed dispersal is more important than the quantity one to determine the dispersal effectiveness of the different dispersers. The recruitment of new *N. tetetzo* individuals occurs beneath the canopies of perennial nurse plants (Valiente-Banuet and Ezcurra 1991); therefore, the dispersal of intact and viable seeds to these sites is an important step for the population dynamics of this columnar cactus.

The different methods used to determine the quantity and quality components of seed dispersal by birds and bats may affect the estimation of the effectiveness calculated for species in each group. Consequently, the effectiveness of each species of frugivore reported in this study could be over or underestimated and therefore, its comparison among species and its effects on the population dynamics of *N. tetetzo* should be interpreted cautiously. Our results showed that the bat *L. curasoae* presented the highest effectiveness because the frequency of visits and the seed deposition probability under shrubs were higher than those found for the rest of the species. These values were obtained in captivity and it is possible that they could be overestimated. However, considering the results reported by other studies and incorporating them in the estimation of the effectiveness of dispersal gave similar results. For instance, Bizerril and Raw (1998) studied the feeding behavior of two other species of phyllostomids, *Carollia perspicillata* Linnaeus and *Glossophaga soricina* Pallas, in a gallery forest, and found that the mean frequency of visits to *Piper* fruits for both species was 14.2 ± 8.4 per hour. This figure is lower than the frequency of visits reported here for *L. curasoae* (17.9). However, if we consider the estimation reported by these authors in our calculations bats are still the best dispersers of *N. tetetzo* seeds with an effectiveness of 3.17. Howell (1979) studied the foraging behavior of *L. curasoae* in the Sonoran desert, and found that bats spent 3 h flying every night and at around midnight they roosted for 2-3 h. This author also reported that while flying, bats fed in a series of discontinuous bouts of ± 20 min alternating with resting periods of ± 20 min. Considering this information, we estimated that the proportion of time that Howell's bats spent resting each night varied between 70-75%, which is similar to our estimation (72%). In contrast Horner et al. (1998), using radio-transmitters to study the foraging behavior of *L. curasoae* reported that this species spent only 17.5% of its time resting in night roosts. When these two figures (70-75% and 17.5%) were considered in our effectiveness estimations, bats were still the best seed dispersers for *N. tetetzo* seeds. This indicates that the fruit traits of *N. tetetzo* corresponding to a bat-dispersal syndrome (van der Pijl 1982) is a good indicator of what is occurring under natural conditions.

Our results showed that bats removed a higher proportion of seeds and pulp from fruits than birds. However, these bat-ingested seeds decreased their germination percentage and germination rate to 86% and 2.9 seeds germinated day^{-1} respectively. Fleming and Sosa (1994) reported that *L. curasoae* removed 10-80% of the available seeds each night of another columnar cactus (*Pachycereus pringlei*) that grows in the Sonoran desert. In contrast to our results on the germination of bat-ingested seeds, Godínez-Alvarez and Valiente-Banuet (1998) found that *N. tetetzo* seeds under experimental treatments simulating gut passage showed the same germinability than the control treatment.

Godínez-Alvarez and Valiente-Banuet (in press) found that *L. curasoae* feeds on *N. tetetzo* fruits while perched spitting out the majority of seeds beneath perches. These same authors reported that this behavior favors the directed dispersal of seeds to a great variety of habitats including plants, rocks and rock crevices. In the Tehuacán Valley, night-roosts used by *L. curasoae* and *C. mexicana* include the dominant shrubs *Mimosa luisana*, *Caesalpinia melanadenia*, *Cercidium praecox* (Ruíz & Pavón) Harms and the columnar cacti *Neobuxbaumia tetetzo* and *Stenocereus stellatus* (Pfeiffer) Riccob. (A. Rojas-Martínez, unpublished manuscript). Some of these plants have significantly higher numbers of young *N. tetetzo* individuals growing beneath their canopies than expected by chance (Valiente-Banuet et al. 1991).

Our observations showed that predators consume a greater proportion of seeds (78%) compared to dispersers (22%). Seed predation by *Carpodacus mexicanus* decreased the finite rate of increase of the *N. tetetzo* population (0.959), whereas the finite rate of increase (0.99) for all species of seed dispersers acting together did not differed from unity, maintaining the population at equilibrium.

When partially eaten fruits fell down to the ground, seeds could be eaten by coyotes (*C. latrans*), gray-foxes (*U. cinereoargenteus*) and harvester ants (*P. barbatus*) which differed in their population effects. According to our results, *C. latrans* and *U. cinereoargenteus* did not affect seed germination but, considering that these species defecate in open spaces and sometimes in caves, where seed germination and seedling establishment are unlikely, it is possible to assume that they have a negative effect on population dynamics, and that they act as seed predators. On the other hand, field observations and Valiente-Banuet & Ezcurra (1991) indicated that harvester ants were predators that consumed a great proportion of the seeds that fall down to the ground.

Considering its dispersal effectiveness and its impacts on the finite rate of increase of the *N. tetetzo* population, it is possible to argue that *L. curasoae* could represent a key species in the ecology of this columnar cactus because this bat plays an important ecological role not only as seed disperser but also as an effective pollinator. Studying *N. tetetzo* pollination in the Tehuacán Valley, Valiente-Banuet et al. (1996) found that successful fruit and seed production depend on the presence of some bats such as *L. curasoae* and *C. mexicana*, among others. Moreover, studies conducted with other columnar cacti (*Neobuxbaumia mezcalaensis* (Bravo) Backeberg, *Neobuxbaumia macrocephala* (Weber) Dawson, Valiente-Banuet et al. 1997a; *Pachycereus weberi*

(Coult.) Buxb., *Pilosocereus chrysacanthus* (F.A.C. Weber) Byles & Rowley, Valiente-Banuet et al. 1997b; *Stenocereus stellatus* (Pfeiffer) Riccobono, Casas et al. 1999) in the same region have indicated that bats are also necessary for the reproduction of these plants. Field observations on the consumption of columnar cacti fruits by bats have shown that *L. curasoae* also feeds on the fruits of other 17 species, suggesting that seed dispersal by bats should be important in population dynamics and community diversity (A. Rojas-Martínez, unpublished manuscript).

In conclusion, our results indicate that *N. tetetzo* fruits are eaten by several fruit-eating birds and mammals which differ in their effects on seed dispersal success and hence on the population dynamics of this columnar cactus. Of all frugivores, the lesser long-nosed bat (*L. curasoae*) could be considered the legitimate dispersal agent which direct dispersal of seeds to safe sites, representing probably a key species in the columnar cactus forests in central Mexico.

ACKNOWLEDGEMENTS

We thank Ariel Alcántara, Oscar Osorio, Adolfo Vital, Antonio Soriano, Leticia Ríos, Verónica Alvarado and Rocío José for field assistance. Alejandro Casas provided critical reviews on the first draft of the manuscript. The first author particularly wants to thank to Teresa Valverde for her helpful comments and suggestions to improve the final version. This study was supported by Fondo Mexicano para la Conservación de la Naturaleza project A1-97/036, Dirección General de Asuntos del Personal Académico, UNAM project IN-207798 and a grant provided by Programa de Apoyo a las Divisiones de Estudio de Posgrado project 030705 to HGA.

LITERATURE CITED

Alvarez-Buylla, E. and M. Slatkin. 1993. Finding confidence limits on population growth rates: Monte Carlo test of a simple analytic method. Oikos **68**:273-282.

Arizmendi, M. del C. and A. Espinosa de los Monteros. 1996. Avifauna de los bosques de cactáceas columnares del Valle de Tehuacán, Puebla. Acta Zoológica Mexicana (n. s.) **67**:25-46.

Biedenweg, D. W. 1983. Time and energy budgets of the mockingbird (*Mimus polyglottos*) during the breeding season. The Auk **100**:149-160.

Bizerril, M. X. A. and A. Raw. 1998. Feeding behaviour of bats and the dispersal of *Piper arboreum* seeds in Brazil. Journal of Tropical Ecology **14**:109-114.

Brunet, J. 1967. Geologic studies. Pages 66-90 *in* D. S. Byers, editor. The prehistory of the Tehuacan Valley. Vol. One. Environment and subsistence. University of Texas Press, Austin, USA.

Casas, A., A. Valiente-Banuet, A. Rojas-Martínez, and P. Dávila. 1999. Reproductive biology and the process of domestication of the columnar cactus *Stenocereus stellatus* in Central Mexico. American Journal of Botany **86**:534-542.

Chavez-Ramirez, F. and R. D. Slack. 1994. Effects of avian foraging and post-foraging behavior on seed dispersal patterns of Ashe juniper. OIKOS **71**:40-46.

Cochran, M. E. and S. Ellner. 1992. Simple methods for calculating age-based life history parameters for stage-structured populations. Ecological Monographs **62**:345-364.

Crawley, M. J. 1993. GLIM for Ecologists. Blackwell Science, Cambridge.

Fleming, T. H. and V. J. Sosa. 1994. Effects of nectarivorous and frugivorous mammals on reproductive success of plants. Journal of Mammalogy **75**:845-851.

García, E. 1973. Modificaciones al sistema de clasificación climática de Köppen. Instituto de Geografía, Universidad Nacional Autónoma de México, México.

Godínez-Alvarez, H. and A. Valiente-Banuet. 1998. Germination and early seedling growth of Tehuacán Valley cacti species: the role of seed ingestion by dispersers and soils on seedling growth. Journal of Arid Environments **39**:21-31.

Godínez-Alvarez, H., A. Valiente-Banuet, and L. Valiente Banuet. 1999. Biotic interactions and the population dynamics of the long-lived columnar cactus *Neobuxbaumia tetetzo* in the Tehuacán Valley, Mexico. Canadian Journal of Botany **77**:203-208.

Godínez-Alvarez, H. and A. Valiente-Banuet. in press. Fruit-feeding behavior of *Leptonycteris curasoae* and *Choeronycteris mexicana* in flight cage experiments: consequences for dispersal of columnar cactus seeds. Biotropica.

Hailman, J. P. 1960. A field study of the mockingbirds´s wing-flashing behavior and its association with foraging. Wilson Bulletin **72**:346-357.

Hendricks, P., J. R. McAuliffe, and A. Valiente-Banuet. 1990. On communal roosting and associated winter social behavior of gray-breasted woodpeckers. The Condor **92**:254-255.

Herrera, C. M., P. Jordano, L. López-Soria, and J. A. Amat. 1994. Recruitment of a mast-fruiting, bird dispersed tree: bridging frugivore activity and seedling establishment. Ecological Monographs **64**:315-344.

Horner, M. A., T. H. Fleming, and C. T. Sahley. 1998. Foraging behaviour and energetics of a nectar-feeding bat, *Leptonycteris curasoae* (Chiroptera: Phyllostomidae). Journal of Zoology, London **244**:575-586.

Howell, D. J. 1979. Flock foraging in nectar-feeding bats: advantages to the bats and to the host plants. The American Naturalist **114**:23-49.

Hutto, R. L., J. R. McAuliffe, and L. Hogan. 1986a. Distributional associates of the Saguaro (*Camegiea gigantea*). The Southwestern Naturalist **31**:469-476.

Hutto, R. L., S. M. Pletschet, and P. Hendricks. 1986b. A fixed-radius point count method for nonbreeding and breeding season use. The Auk **103**:593-602.

Joern, W. T. and J. F. Jackson. 1983. Homogeneity of vegetational cover around the nest and avoidance of nest predation in mockingbirds. The Auk **79**:497-499.

Jordano, P. 1992. Fruits and frugivory. Pages 105-156 *in* M. Fenner, editor. Seeds: the ecology of regeneration in plant communities. CAB International, Wallingford, U. K.

Loiselle, B. A. and J. G. Blake. 1999. Dispersal of melastome seeds by fruit-eating birds of tropical forest understory. Ecology **80**:330-336.

Olin, G., S. M. Alcorn, and J. M. Alcorn. 1989. Dispersal of viable saguaro seeds by white-winged dove (*Zenaida asiatica*). The Southwestern Naturalist **34**:282-284.

Osorio, B. O., A. Valiente-Banuet, P. Dávila, and R. Medina. 1996. Tipos de vegetación y diversidad β en el Valle de Zapotitlán de las Salinas, Puebla, México. Boletín de la Sociedad Botánica de México **59**: 35-36.

Reid, N. 1989. Dispersal of mistletoes by honeyeaters and flowerpeckers: components of seed dispersal quality. Ecology **70**:137-145.

Rojas-Martínez, A. and A. Valiente-Banuet. 1996. Análisis comparativo de la quiropterofauna del Valle de Tehuacán-Cuicatlán, Puebla-Oaxaca. Acta Zoológica Mexicana (n. s.) **67**:1-23.

Rzedowski, J. 1978. Vegetación de México. Ed. Limusa, México.

Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio **107/108**:15-29.

Shreve, F. 1931. Physical conditions in sun and shade. Ecology **12**:96-104.

Smith, C. E. 1965. Flora of Tehuacan Valley. Fieldiana Botany **31**:107-143.

Steenbergh, W. H. and C. H. Lowe. 1969. Critical factors during the first years of life of the saguaro (*Cereus giganteus*) at the Saguaro National Monument, Arizona. Ecology **50**:825-834.

———— . 1977. Ecology of the Saguaro: II. Reproduction, Germination, Establishment, Growth and Survival of the Young Plant. Available from the National Park Service Scientific Monograph Series 8. U. S. Government Printing Office, Washington, DC.

Sun, C., A. R. Ives, H. J. Kraeuter, and T. C. Moermond. 1997. Effectiveness of three turacos as seed dispersers in a tropical montane forest. Oecologia **112**:94-103.

Turner, R. M., S. M. Alcorn, G. Olin, and J. A. Booth. 1966. The influence of shade, soil and water on saguaro seedling establishment. Botanical Gazette **127**:95-102.

Valiente-Banuet, A. and E. Ezcurra. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse-plant *Mimosa luisana* in the Tehuacán Valley, Mexico. Journal of Ecology **79**:961-971.

Valiente-Banuet, A., O. Briones, A. Bolongaro-Crevenna, E. Ezcurra, M. Rosas, H. Núñez, G. Barnard, and E. Vázquez. 1991. Spatial relationships between cacti and nurse shrubs in a semi-arid environment in central Mexico. Journal of Vegetation Science **2**:15-20.

Valiente-Banuet, A., M. del C. Arizmendi, A. Rojas-Martínez, and L. Domínguez-Canseco. 1996. Ecological relationships between columnar cacti and nectar feeding bats in Mexico. Journal of Tropical Ecology **12**:103-119.

Valiente-Banuet, A., A. Rojas-Martínez, M. del C. Arizmendi, and P. Dávila. 1997a. Pollination biology of two columnar cacti (*Neobuxbaumia mezcalaensis* and *Neobuxbaumia macrocephala*) in the Tehuacán Valley, central Mexico. American Journal of Botany **84**:452-455.

Valiente-Banuet, A., A. Rojas-Martínez, A. Casas, M. del C. Arizmendi, and P. Dávila. 1997b. Pollination biology of two winter-blooming giant columnar cacti in the Tehuacán Valley, central Mexico. Journal of Arid Environments **37**:331-341.

van der Pijl, L. 1982. Principles of dispersal in higher plants. Springer-Verlag. Berlin.

Table 1. Matrix model of *Neobuxbaumia tetetzo* used to simulate the effect of seed removal by different species of frugivores on the finite rate of increase.

	se1	se2	se3	sa	j	im	m1	m2	m3	m4	m5	m6
se1	0.628							0.22	0.39	0.58	0.74	0.76
se2	0.057	0.707										
se3		0.175	0.703									
sa			0.196	0.895								
j				0.091	0.916							
im					0.073	0.959						
m1						0.041	0.94					
m2							0.06	0.925				
m3								0.057	0.93			
m4									0.059	0.952		
m5										0.048	0.822	
m6											0.107	0.949

The size categories are as follows: se1, 0-2 cm; se2, 2-8 cm; se3, 8-15 cm; sa, 15-45 cm; j, 45-100 cm; im, 100-150 cm; m1, 150-250 cm; m2, 250-350 cm; m3, 350-450 cm; m4, 450-550 cm; m5, 550-650 cm; m6, >650 cm.

Table 2. Relative abundance for different frugivorous birds (individuals h^{-1}) and bats (individuals h^{-1} net^{-1}) that eat *N. tetetzo* fruits in the Tehuacán Valley, Mexico.

Frugivore species	Family	Relative abundance
Zenaida asiatica†	Columbidae	37.2
Carpodacus mexicanus†	Fringillidae	30.3
Mimus polyglottos†	Mimidae	12.5
Campylorhynchus brunneicapillus†	Troglodytidae	11.7
Melanerpes hypopolius†	Picidae	10.2
Aimophila mystacalis†	Emberizidae	6.9
Toxostoma curvirostre†	Mimidae	2.4
Cyanocompsa cyanoides†	Emberizidae	1.0
Leptonycteris curasoae‡	Phyllostomidae	0.36
Choeronycteris mexicana‡	Phyllostomidae	0.29
Picoides scalaris†	Picidae	0.20
Artibeus jamaicensis‡	Phyllostomidae	0.11
Passerina versicolor†	Emberizidae	0.06
Carduelis psaltria†	Fringillidae	0.06

† Birds. Total observation time 15 h.

‡ Bats. Total netting effort 1543 h/net.

Table 3. Data on visits made to *N. tetetzo* fruits by different frugivorous birds in the Tehuacán Valley, Mexico.

Bird species	Number	Frequency (h^{-1})	Duration ± S. D. (min)
Carpodacus mexicanus	116	1.84	2.1 ± 2.9
Zenaida asiatica	66	1.04	2.3 ± 3.6
Melanerpes hypopolius	27	0.43	0.9 ± 0.7
Cyanocompsa cyanoides	11	0.17	1.4 ± 1.2
Toxostoma curvirostre	9	0.14	2.2 ± 1.8
Campylorhynchus brunneicapillus	7	0.11	0.6 ± 0.5
Mimus polyglottos	7	0.11	4.0 ± 4.0
Picoides scalaris	7	0.11	0.8 ± 0.6
Total observation time (h)	63.2		
Global frequency of visits (visits/h)	4.0		

Table 4. Frugivore effects on seed germination of *N. tetetzo* after gut passage and logistic regression parameters (*a*=intercept, *b*=germination rate, *k*=maximum number of germinated seeds) fitted to germination curves.

Frugivorous species	Germination[†] (%)	*a*	*b* (95% limits)	*K*	F[‡]	R^2
Campylorhynchus brunneicapillus	97.5 a	-8.1	3.2 (2.8, 3.6)	47.8	4057.8	0.99
Toxostoma curvirostre	97.5 a	-8.7	3.4 (2.9, 4.0)	48.2	2625.3	0.99
Mimus polyglottos	97.3 a	-9.9	5.7 (0.7, 10.6)	48.7	632.7	0.99
Melanerpes hypopolius	95.5 a	-8.3	4.6 (-1.6, 10.7)	46.9	592.9	0.91
Leptonycteris curasoae	86.0 b	-5.6	2.9 (1.1, 4.6)	21.1	500.3	0.93
Urocyon cinereoargenteus	79.5 b	-4.8	1.4 (1.1, 1.7)	39.1	1792.3	0.98
Canis latrans	46.7 c	-6.7	1.2 (0.6, 1.8)	21.9	261.5	0.91
Aimophyla mystacalis	15.0 d	-3.0	1.0 (-0.4, 2.4)	3.9	22.3	0.38

[†] Numbers with the same letter did not differ significantly ($p<0.05$).

[‡] All values were significant ($p<0.00001$).

Table 5. Number of visits to different landing plant categories and deposition probability of seeds by birds in the Tehuacán Valley, Mexico. Numbers in parentheses indicate expected values by chance. Figures after specific names referred to the number of individuals observed in each species.

Bird species	*N. tetetzo*	Shrubs	Others	Total
Melanerpes hypopolius (24)	135 (88)*	5 (42)*	16 (26)	156
	0.87	0.03	0.1	
Mimus polyglottos (38)	111 (204)*	174 (99)*	78 (60)*	363
	0.31	0.48	0.21	
Zenaida asiatica (20)	86 (62)*	4 (30)*	21 (18)	111
	0.77	0.04	0.19	
Toxostoma curvirostre (11)	50 (38)	8 (19)*	10 (11)	68
	0.73	0.12	0.15	
Carpodacus mexicanus (18)	48 (38)	12 (18)	7 (11)	67
	0.72	0.18	0.1	
Campylorhynchus brunneicapillus (7)	17 (17)	13 (8)	0 (5)	30
	0.57	0.43	0	
Cyanocompsa cyanoides (5)	9 (10)	6 (5)	3 (3)	18
	0.5	0.33	0.17	
Total	456	222	135	813

* denote significant differences between observed and expected values (*G* = 259.5, d.f. 12, $p < 0.00001$).

Table 6. Dispersal effectiveness for different frugivores that fed on *N. tetetzo* fruits in the Tehuacán Valley, Mexico.

Frugivores	Relative abundance	Frequency of visits	Seed germination	Deposition probability	Effectiveness
Leptonycteris curasoae	0.36	17.9	0.86	0.72	3.99
Mimus polyglottos	12.5	0.11	0.973	0.48	0.65
Campylorhynchus brunneicapillus	11.7	0.11	0.975	0.43	0.55
Melanerpes hypopolius	10.2	0.43	0.955	0.03	0.13
Toxostoma curvirostre	2.4	0.14	0.975	0.12	0.04
Carpodacus mexicanus	30.3	1.84	0	0.18	0
Zenaida asiatica	37.2	1.04	0	0.04	0

Notes: Effectiveness = relative abundance x frequency of visits x seed germination x deposition probability under shrubs.

Table 7. Effect of seed dispersal for different species of frugivores used to modify the fecundity values in a one-year projection matrix model of *Neobuxabaumia tetetzo*, and their estimated finite rates of increase.

Frugivores	Seed removal probability	Germination percentage	Deposition probability	Effect of seed dispersal[‡]	Estimated rate of increase (90% limits)
Seed dispersers					
Leptonycteris curasoae	0.159	0.86	0.72	0.098	0.989 (0.937-1.00)
Mimus polyglottos	0.011	0.973	0.48	5.14×10^{-03}	0.974 (0.936-0.999)
Campylorhynchus brunneicapillus	0.011	0.975	0.43	4.6×10^{-03}	0.973 (0.936-0.999)
Melanerpes hypopolius	0.036	0.955	0.03	1.03×10^{-03}	0.968 (0.935-0.999)
Toxostoma curvirostre	0.003	0.975	0.12	3.5×10^{-04}	0.965 (0.935-0.999)
All dispersers[†]	0.22	0.888	0.574	0.112	0.99 (0.937-1.00)
Seed predators					
Carpodacus mexicanus	0.46	0	0.18	0	0.959 (0.923-0.999)
Zenaida asiatica	0.32	0	0.04	0	-
All predators[†]	0.78	0	0.12	0	-

[‡] Effect of seed dispersal = Seed removal * Germination percentage * Deposition probability

[†] All species effects were calculated as follows: 1) Seed removal probability as the sum of all the probabilities estimated for each species, 2) Germination percentage, and 3) Deposition probability as the mean weighted by the probability of seed removal

Figure legends

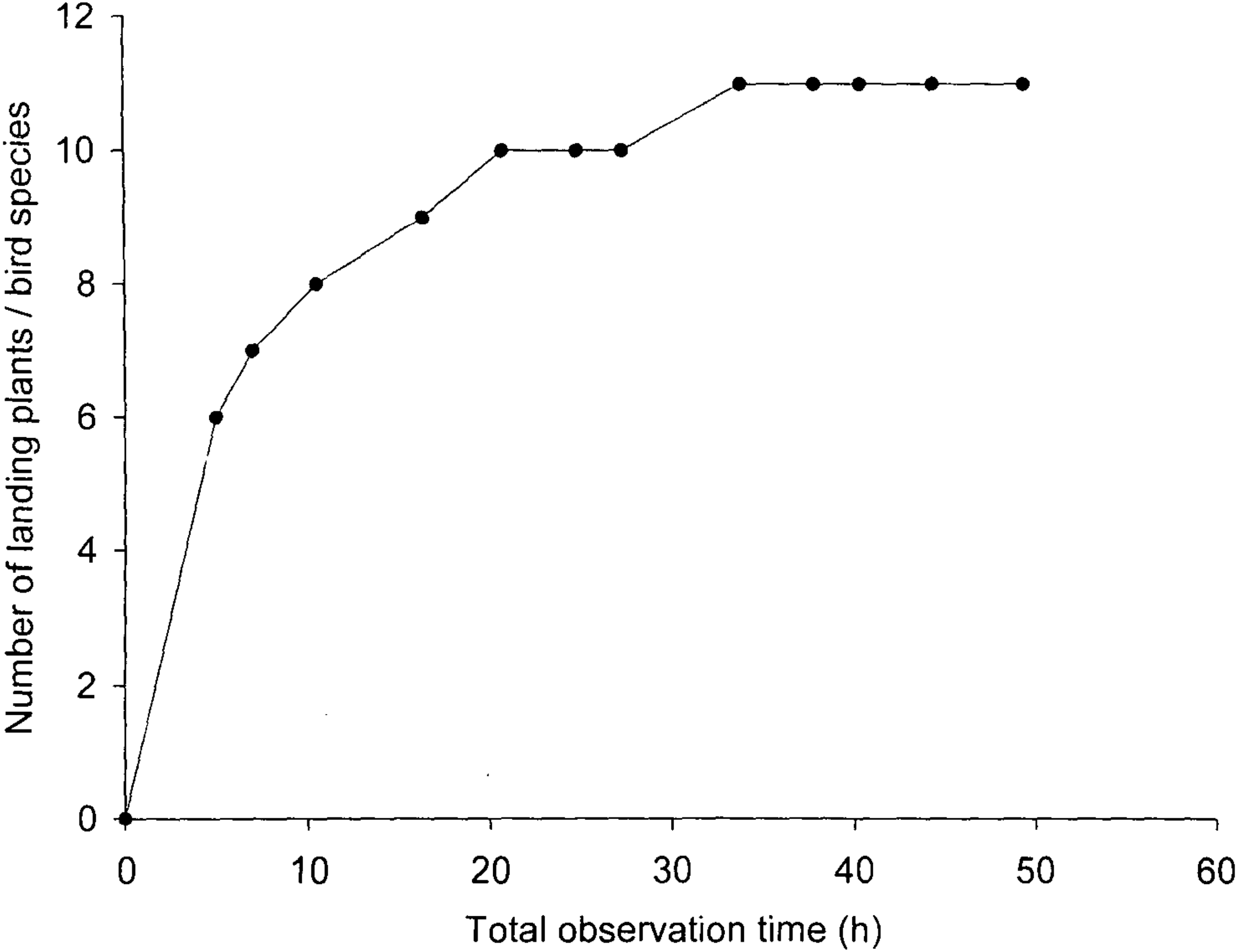
Figure 1. Cumulative number of landing plants observed, after *N. tetetzo* fruit consumption, for different bird species in the Tehuacán Valley, Mexico.

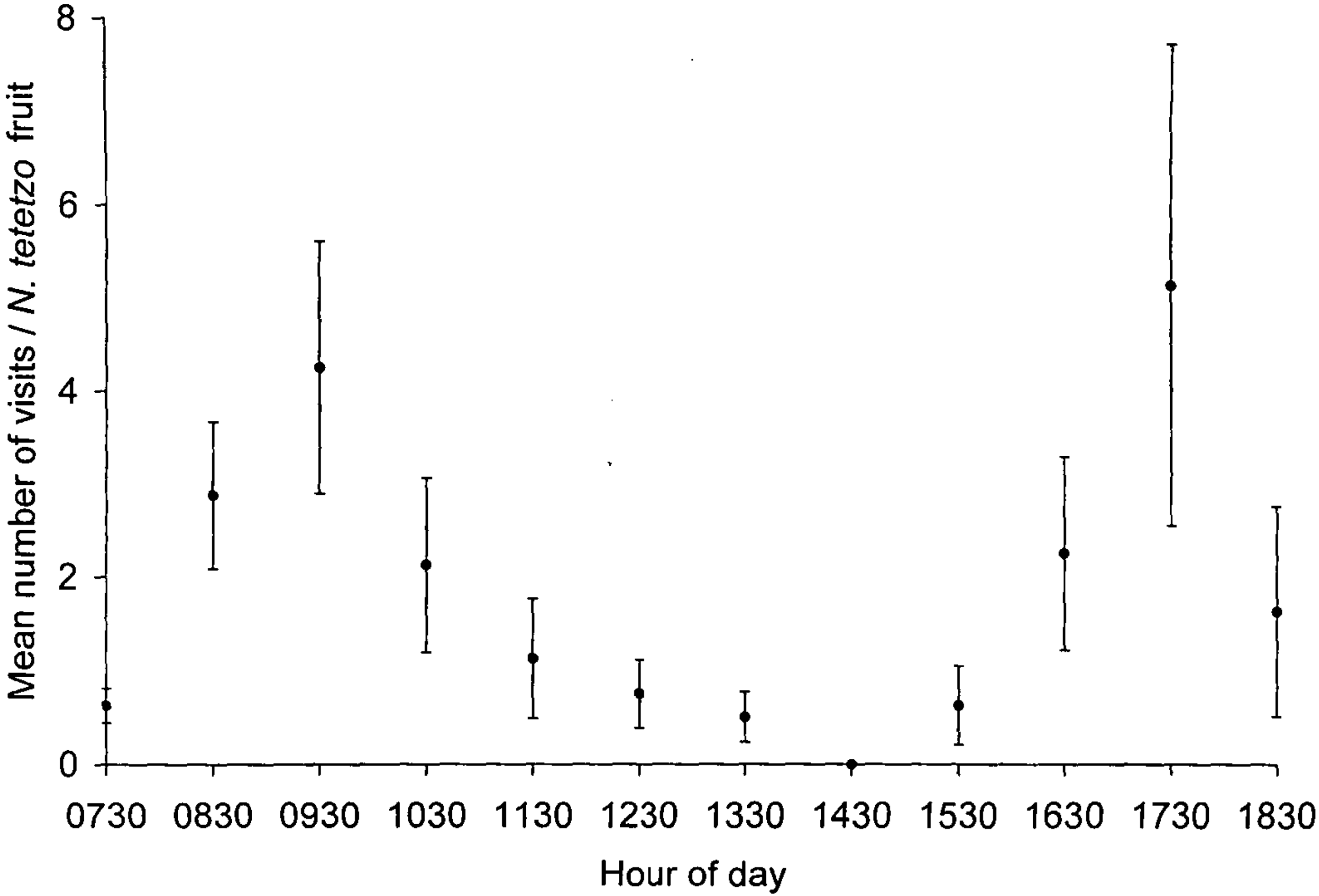
Figure 2. Mean number of visits (± S. E.) to the fruits of *N. tetetzo* throughout the day by different species of birds in the Tehuacán Valley, Mexico. Total observation time was 70 h.

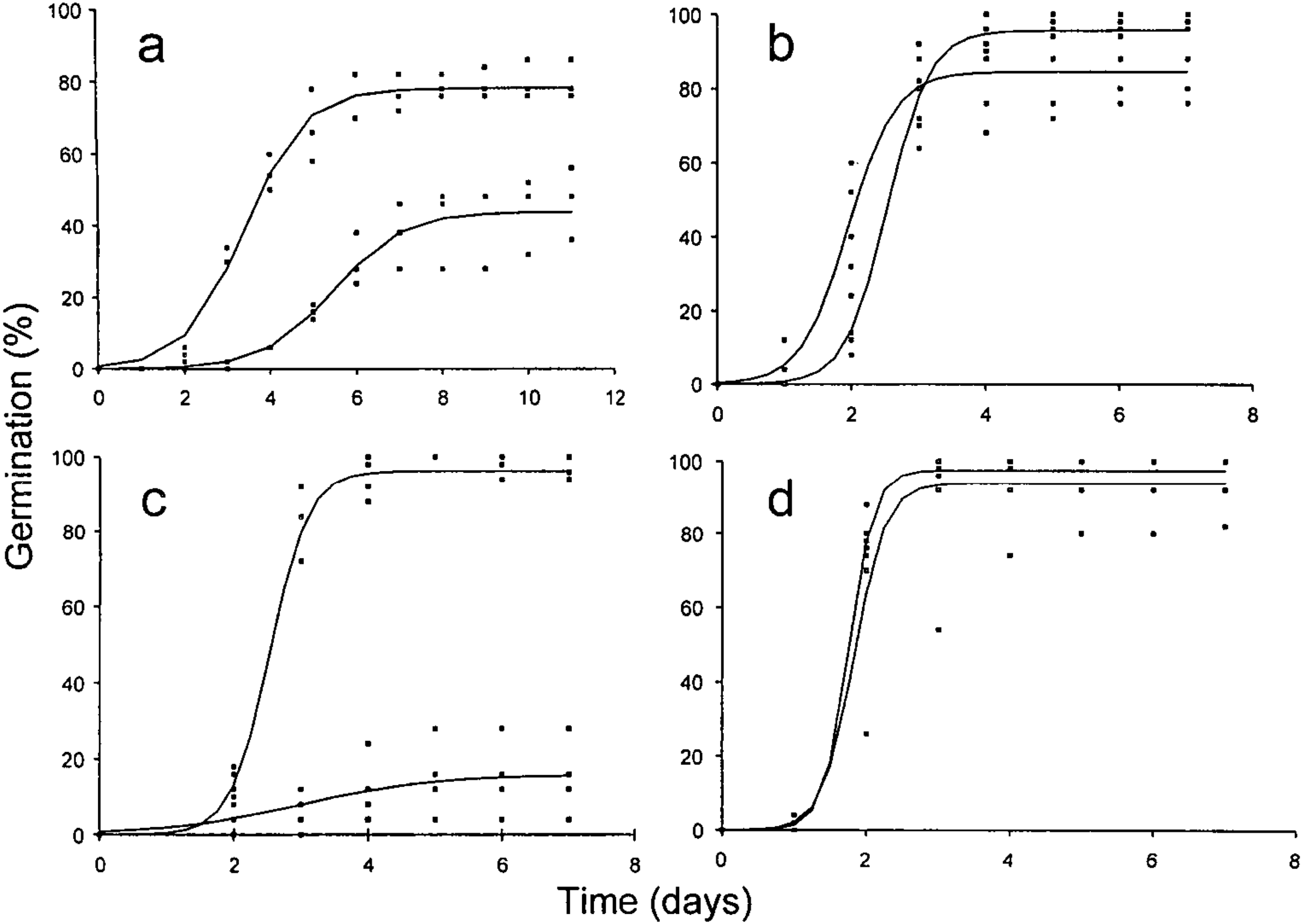
Figure 3. Germination of *N. tetetzo* seeds after gut passage for different species of birds and mammals: a) *Urocyon cinereoargenteus* (■), *Canis latrans* (□); b) *Leptonycteris curasoae* (■), *Campylorhynchus brunneicapillus* (□); c) *Toxostoma curvirostre* (■), *Aimophyla mystacalis* (□); d) *Melanerpes hypopolius* (■), *Mimus polyglottos* (□). Symbols and continued lines refer to data and logistic regressions fitted respectively.

Figure 4. Proportion of pulp and seeds removed from *N. tetetzo* fruits by birds and bats in the Tehuacán Valley, Mexico. Open and closed bars refer to expected and observed values respectively. Asterisks denote significant differences ($G = 38.6$, d. f. 3, $p < 0.00001$).

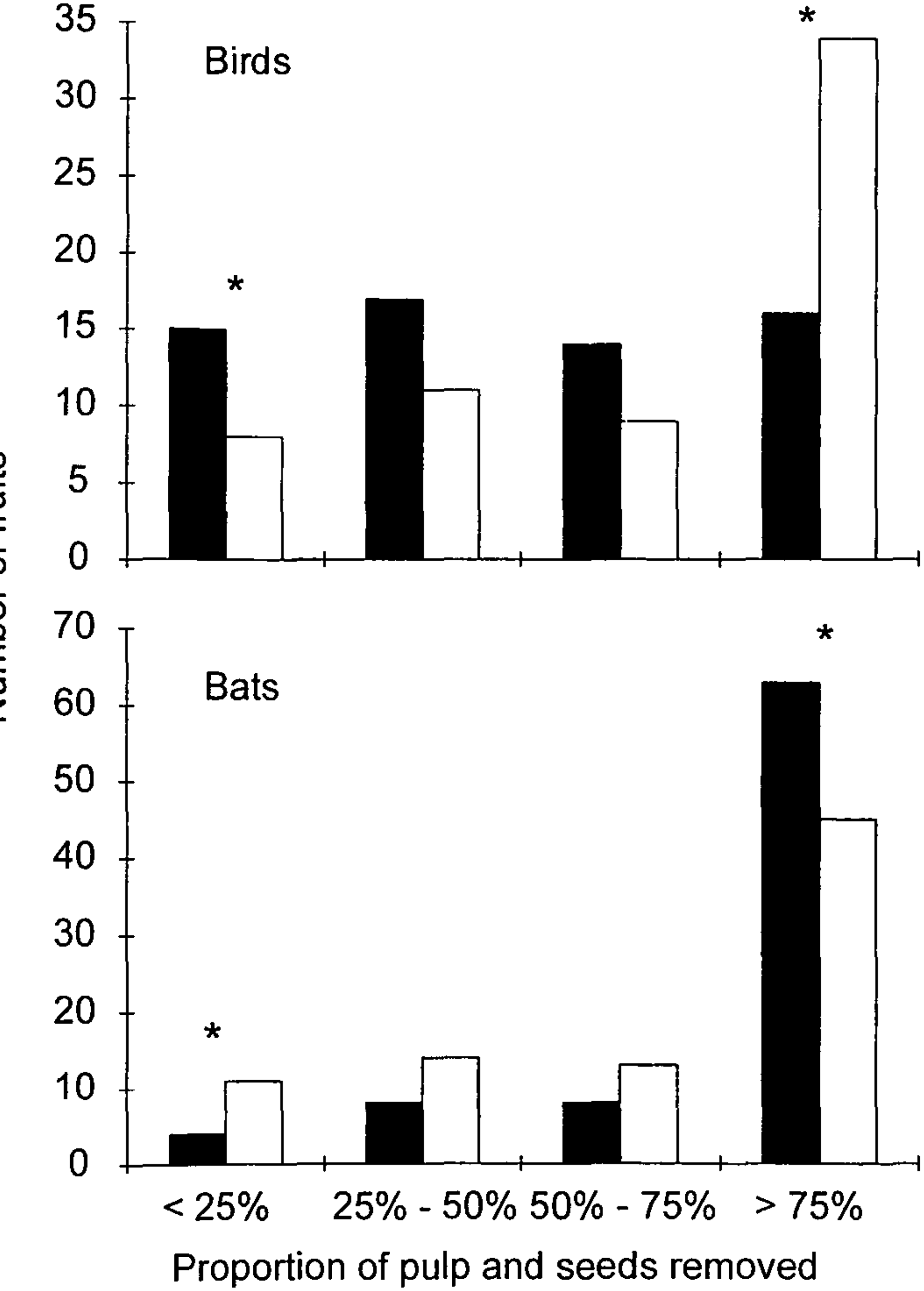
Figure 5. Possible paths for *N. tetetzo* seeds and their effects on the finite rate of increase in the Tehuacán Valley, Mexico. For elements marked with ? effects were not estimated.

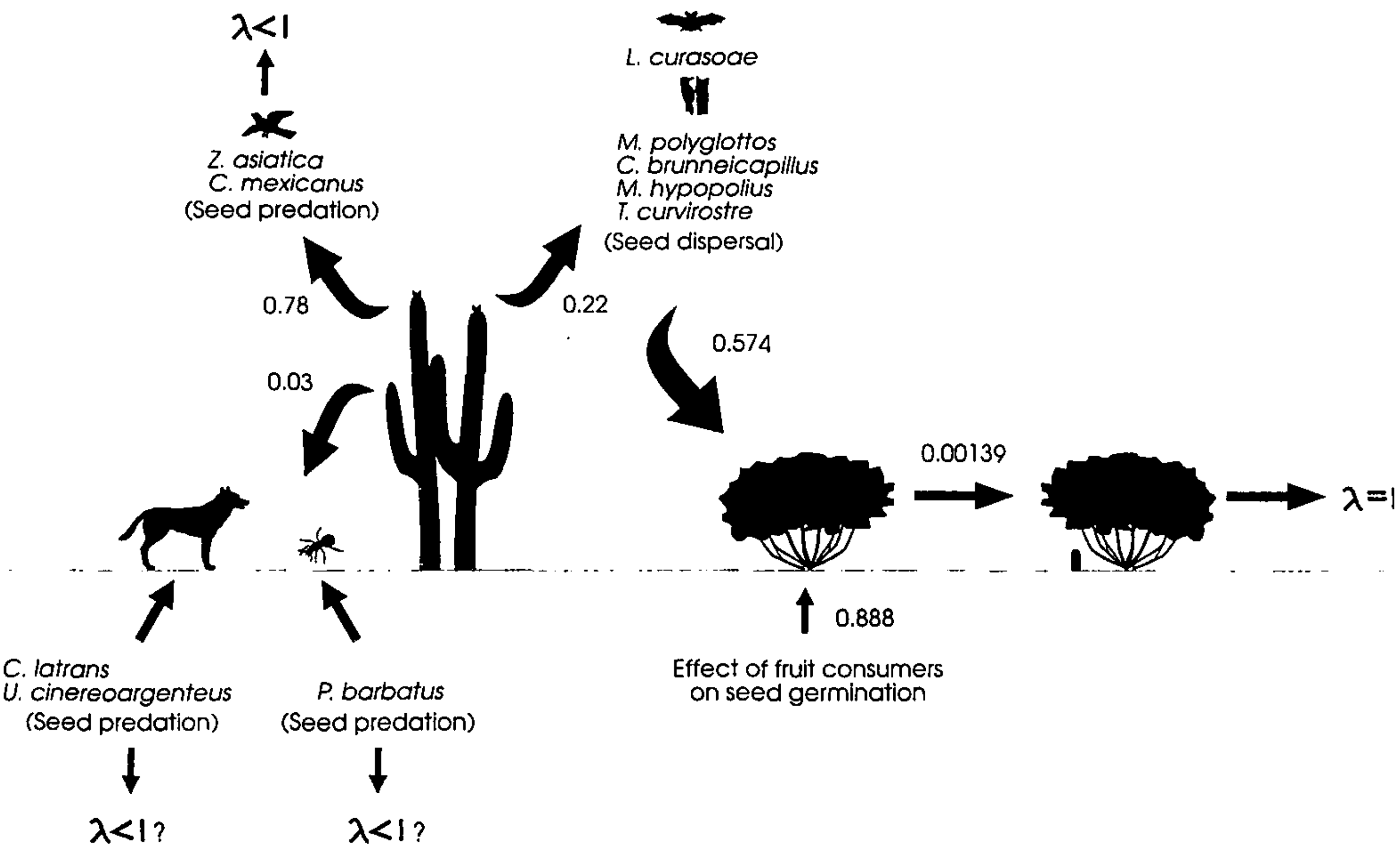

Number of landing plants / bird species
0
2
4
6
8
10
12
0
10
20
30
40
50
60
Total observation time (h)


8
6
4
2
0
Mean number of visits / *N. tetetzo* fruit
0730
0830
0930
1030
1130
1230
1330
1430
1530
1630
1730
1830
Hour of day



a
b
c
d
Germination (%)
Time (days)
0
20
40
60
80
100
0
2
4
6
8
10
12


Birds
Bats
35
30
25
20
15
10
5
0
70
60
50
40
30
20
10
0
*
*
*
*
< 25%
25% - 50%
50% - 75%
> 75%
Proportion of pulp and seeds removed


λ<1
Z. asiatica
C. mexicanus
(Seed predation)
L. curasoae
M. polyglottos
C. brunneicapillus
M. hypopolius
T. curvirostre
(Seed dispersal)
0.78
0.22
0.574
0.03
0.00139
λ=1
0.888
Effect of fruit consumers on seed germination
C. latrans
U. cinereoargenteus
(Seed predation)
P. barbatus
(Seed predation)
λ<1?
λ<1?

DISCUSION

Las cactáceas columnares muestran una estrecha interrelación con otras especies con las que coexisten en las comunidades en las que habitan. Los parámetros demográficos como la sobrevivencia, el crecimiento y la reproducción de *N. tetetzo* indican inequívocamente que éstos son afectados por diferentes procesos de interacción ecológica entre plantas y/o entre plantas y animales como son el nodricismo (Valiente-Banuet 1991, Valiente-Banuet & Ezcurra 1991), la competencia (Valiente-Banuet *et al.* 1991, Flores-Martínez *et al.* 1994, 1998), la polinización (Valiente-Banuet *et al.* 1996) y la dispersión, entre otras.

Diversos trabajos en la literatura de los desiertos habían sugerido ya previamente que la dispersión de las semillas por animales es un proceso importante en la ecología de estos ecosistemas y, en particular, en la ecología de las cactáceas columnares (Hutto *et al.* 1986, McAuliffe, 1988, Olin *et al.* 1989, Valiente-Banuet *et al.* 1996). Los resultados obtenidos en el presente trabajo muestran claramente que la interacción entre los animales frugívoros y la cactácea columnar *N. tetetzo* constituye un puente de enlace fundamental entre la reproducción de los organismos adultos y la fase de establecimiento de plántulas.

Las simulaciones del efecto de los dispersores sobre la tasa finita de crecimiento o lambda mostraron que las distintas especies de animales que se alimentan de los frutos pueden actuar como depredadores o dispersores de semillas con distintos grados de efectividad, afectando la población de *N. tetetzo* de distintas maneras. En particular, el murciélago *L. curasoae* es la especie con el mayor efecto dado que es capaz de transportar las semillas, con mayor probabilidad, a sitios seguros debajo de la copa de árboles y arbustos. Estos resultados sugieren que este murciélago puede ser considerado como una especie clave (*i.e.* keystone species) en la ecología de las comunidades de zonas áridas, dada la gran abundancia de cactáceas columnares. Esta idea es apoyada también por los resultados encontrados por Valiente-Banuet *et al.* (1996) sobre la polinización de *N. tetetzo*; en los cuales se muestra que la producción de frutos y semillas depende única y exclusivamente de la presencia de tres especies de murciélagos entre los que se encuentra *L. curasoae*. Esta evidencia indica que el éxito reproductivo de *N. tetetzo* depende en gran medida de la participación de *L. curasoae*. Si además de lo anterior, se considera que la presencia de *L. curasoae* en el Valle de Tehuacán es estacional debido a sus movimientos migratorios altitudinales (Rojas-Martínez *et al.* en prensa) su papel como especie clave adquiere mayor relevancia.

Las características de los frutos de *N. tetetzo* corresponden a las reportadas para el síndrome de quiropterocoria (van der Pijl 1982). Estas características sugieren que el murciélago *L. curasoae* es el principal agente dispersor de las semillas de esta planta y que la interacción que se establece entre ambos grupos ha generado procesos de selección natural a lo largo del tiempo los cuales determinan las características actuales de los frutos (Abrahmson 1989). Los resultados reportados en este trabajo así como los resultados obtenidos en los estudios de polinización (Valiente-Banuet *et al.* 1996) apoyan esta hipótesis. Sin embargo, es necesario considerar que el proceso coevolutivo que se establece en la dispersión es difuso (Wheelwright & Orians 1982) y que algunas de las características observadas en los frutos no son adaptaciones sino que pueden ser el resultado de factores históricos o filogenéticos, entre otros (Herrera 1992, Jordano 1995). En este sentido, es necesario realizar estudios que permitan determinar si las características de los frutos de *N. tetetzo* pueden ser consideradas como adaptaciones producidas por la interacción con el murciélago *L. curasoae* o bien, como resultado de la filogenia.

Estudios realizados sobre la polinización en diversas especies de cactáceas columnares del Valle de Tehuacán, mostraron que la producción exitosa de frutos y semillas de estas plantas depende de la participación de distintas especies de aves y murciélagos (Valiente-Banuet *et al.* 1996, 1997a, 1997b). Considerando la gran diversidad de estos grupos en la región (para información específica sobre cada uno de los grupos ver Dávila *et al.* 1993, cactáceas columnares; Rojas-Martínez & Valiente-Banuet 1996, murciélagos; Arizmendi & Espinosa de los Monteros 1996, aves), es posible suponer que el consumo de los frutos y la dispersión de las semillas deben jugar un papel importante no sólo en la dinámica poblacional de las especies involucradas sino también en el mantenimiento de la diversidad de estos ecosistemas. Observaciones previas realizadas sobre el consumo de frutos de cactáceas columnares por murciélagos de la familia Phyllostomidae mostraron que aproximadamente 17 especies son consumidas por al menos 5 especies de murciélagos, sugiriendo que los murciélagos podrían ser los dispersores potenciales de un gran número de especies y afectar así la composición de la comunidad (Rojas-Martínez *et al.* in prep). Sin embargo, es necesario realizar estudios sobre la dispersión de las semillas en otras especies de cactáceas columnares que permitan determinar la importancia de las distintas especies de frugívoros en dicho proceso. La generación de esta información es fundamental ya que con ella será posible construir la matriz de interacciones de la comunidad para determinar las especies, de aves y murciélagos, más relevantes que podrían afectar a otras especies de plantas y cómo se modifican dichas interacciones cuando se consideran todas las especies que conforman el ecosistema (Jordano 1987).

Los resultados presentados en este estudio documentan el efecto que los dispersores tienen sobre la dinámica poblacional de *N. tetetzo* considerando la información generada durante los años de 1996 y 1997. Sin embargo, las cactáceas columnares son plantas longevas que pueden vivir entre 125 y 175 años (Steenbergh & Lowe 1977) por lo que su dinámica poblacional depende del balance entre diversos factores bióticos y abióticos el cual ocurre en el largo plazo (*i. e.* décadas; Pierson & Turner 1998). En este sentido, para tener una estimación real del efecto de la dispersión sobre la demografía de estas plantas es esencial llevar a cabo estudios de largo plazo que consideren la variación anual en la producción de los frutos, las variaciones en la abundancia de las principales especies de frugívoros y su efecto sobre la tasa de crecimiento de la población. Estudios recientes realizados en el matorral mediterráneo han mostrado que la dispersión de semillas por animales es una interacción muy dinámica con una gran variabilidad anual por lo que para comprenderla totalmente es necesario realizar estudios de largo plazo (Herrera 1998).

En términos generales, el presente trabajo aporta evidencia que apoya la idea de que el estudio de las interacciones bióticas es necesario para el entendimiento de la ecología de las zonas áridas y semiáridas. En particular, el estudio de las interacciones positivas como la facilitación, la polinización y la dispersión promete ser un área relevante en el entendimiento de los sistemas con un alto estrés ambiental (Callaway & Walker 1997, Hacker & Gaines 1997, Holmgren *et al.* 1997). Considerando los resultados de este trabajo es posible afirmar también que la dispersión de las semillas por animales es un proceso relevante que afecta la ecología y la evolución de la cactácea columnar *Neobuxbaumia tetetzo*. Esta interacción no sólo determina, en gran medida, su éxito reproductivo sino que además afecta su dinámica poblacional y su patrón de distribución espacial. En el futuro, el estudio de esta interacción y sus efectos en otras especies de cactáceas columnares será un campo que permitirá evaluar la relevancia de los frugívoros a nivel comunitario. Para cumplir con estos objetivos es necesario realizar estudios de largo plazo que consideren las variaciones anuales en la interacción y sus efectos.

REFERENCIAS

Abrahamson, W.C. 1989. Plant-animal interactions: an overview. In: Abrahamson, W.C. (ed). *Plant-Animal Interactions*. McGraw-Hill Book Company.

Arizmendi, M. del C. & Espinosa de los Monteros, A. 1996. Avifauna de los bosques de cactáceas columnares del Valle de Tehuacán, Puebla. *Acta Zoológica Mexicana* (n. s.) 67:25-46.

Callaway, R. & Walker, L. R. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78(7):1958-1965.

Dávila, A. P., Villaseñor, J. L., Medina, L. R., Ramirez, R. A., Salinas, T. A., Sánchez-Ken, J. & Tenorio, L. P. 1993. *Listados florísticos de México X. Flora del Valle de Tehuacán-Cuicatlán.* Instituto de Biología. UNAM. México.

Flores-Martínez, A., Ezcurra, E. & Sánchez-Colón, S. 1994. Effect of *Neobuxbaumia tetetzo* on growth and fecundity of its nurse plant *Mimosa luisana. Journal of Ecology* 82:325-330.

Flores-Martinez, A., Ezcurra, E. & Sánchez-Colón, S. 1998. Water availability and the competitive effect of a columnar cactus on its nurse plant. *Acta Oecologica* 19(1):1-8.

Hacker, S. D. & Gaines, S. D. 1997. Some implications of direct positive interactions for community species diversity. *Ecology* 78(7):1990-2003.

Herrera, C. M. 1992. Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in mediterranean woody plants. *The American Naturalist* 140(3):421-446.

Herrera, C. M. 1998. Long-term dynamics of mediterranean frugivorous birds and fleshy fruits: A 12-year study. *Ecological Monographs* 68(4):511-538.

Holmgren, M., Scheffer, M. & Huston, M. A. 1997. The interplay of facilitation and competition in plant communities. *Ecology* 78(7):1966-1975.

Hutto, R. L., McAuliffe, J. R. & Hogan, L. 1986. Distributional associates of the Saguaro (*Carnegiea gigantea*). *The Southwestern Naturalist* 31(4):469-476.

Jordano, P. 1987. Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. *The American Naturalist* 129(5):657-677.

Jordano, P. 1995. Angiosperm fleshy fruits and seed dispersers: A comparative analysis of adaptation and constraints in plant-animal interactions. *The American Naturalist* 145(2):163-191.

McAuliffe, J. R. 1988. Markovian dynamics of simple and complex desert plant communities. *The American Naturalist* 131(4):459-490.

Olin, G., Alcorn, S. M. & Alcorn, J. M. 1989. Dispersal of viable saguaro seeds by white-winged doves (*Zenaida asiatica*). *The Southwestern Naturalist* 34:282-284.

Pierson, E. A. & Turner, R. M. 1998. An 85-year study of saguaro (*Carnegiea gigantea*) demography. *Ecology* 79(8):2676-2693.

Rojas-Martinez, A. & Valiente-Banuet, A. 1996. Análisis comparativo de la quiropterofauna del Valle de Tehuacán-Cuicatlán, Puebla-Oaxaca. *Acta Zoológica Mexicana* (n. s.) 67:1-23.

Rojas-Martínez, A., Valiente-Banuet, A., Arizmendi, M. del C., Alcántara-Eguren, A. & Arita, H. en prensa. Seasonal distribution of the long-nosed bat (*Leptonycteris curasoae*) in North America: Does a generalized migration pattern really exist?. *Journal of Biogeography.*

Rojas-Martínez, A., Godínez-Alvarez, H., Valiente-Banuet, A., Arizmendi, M. del C. & Soriano, A. in prep. Columnar cacti fruits: an important food resource for phyllostomid bats in the Tehuacán Valley, Mexico.

Steenbergh, W. F. & Lowe, C. H. 1977. Ecology of the saguaro II. Reproduction, germination establishment, growth and survival of the young plant. *Nat. Park Serv. Sci. Monogr. Ser. No. 8. Washington, D. C.*

Valiente Banuet, A. 1991. Dinámica del establecimiento de cactáceas: Patrones generales y consecuencias de los procesos de facilitación por plantas nodriza en desiertos. *Tesis de Doctorado. Centro de Ecología, UNAM. México.*

Valiente-Banuet, A., Bolongaro-Crevenna, A., Briones, O., Ezcurra, E., Rosas, M., Núñez, H., Barnard, G. & Vázquez, E. 1991. Spatial relationships between cacti and nurse shrubs in a semi-arid environment in central Mexico. *Journal of Vegetation Science* 2:15-20.

Valiente-Banuet, A. & Ezcurra, E. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán Valley, Mexico. *Journal of Ecology* 79:961-971.

Valiente-Banuet, A., Arizmendi, M. del C., Rojas-Martínez, A. & Domínguez, L. 1996. Ecological relationships between columnar cacti and nectar-feeding bats in Mexico. *Journal of Tropical Ecology* 12:103-119.

Valiente-Banuet, A., Rojas-Martínez, A., Arizmendi, M. del C. & Dávila, P. 1997a. Pollination biology of two columnar cacti (*Neobuxbaumia mezcalaensis* and *Neobuxbaumia macrocephala*) in the Tehuacán Valley, central Mexico. *American Journal of Botany* 84(4):452-455.

Valiente-Banuet, A., Rojas-Martínez, A., Casas, A., Arizmendi, M. del C. & Dávila, P. 1997b. Pollination biology of two winter-blooming giant columnar cacti in the Tehuacán Valley, central Mexico. *Journal of Arid Environments* 37:331-341.

van der Pijl, L. 1982. *Principles of dispersal in higher plants.* Springer-Verlag. Berlin.

Wheelwright, N. T. & Orians, G. H. 1982. Seed dispersal by animals: Contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *The American Naturalist* 119(3):402-413.