Munibe (Ciencias Naturales-Natur Zientziak) • No. 57 (2009) • 185-194 • ISSN 0214-7688

The lizard *Podarcis lilfordi* as a potential disperser of the Solanaceae plant *Lycopersicon esculentum*: Can legitimate dispersers indirectly promote plant invasions?

M. Aurora Castilla [1*, 2]

Abstract

I examined, under laboratory conditions, the effect of the Balearic lizard *Podarcis lilfordi*, on germination performance of the plant *Lycopersicon esculentum* (Solanaceae). The time of germination was significantly reduced after ingestion by lizards, but the final percentage of germination (after 10 days) did not differ between seeds consumed by lizards (91 %) and those not ingested (98 %). The amplitude of daily temperature fluctuations to which seeds were exposed had a significant effect on germination time, but not on the final percentage of germination. Small daily temperature fluctuations (± 3,5 °C) reduced germination time compared to larger ones (± 5,7 °C). Because *P. lilfordi* improves germination performance of *L. esculentum*, this lizard is a legitimate and efficient disperser of this plant. I also discuss how legitimate dispersers can be potential agents for the introduction of alien plants in association with human activities.

• **Palabras clave:** plant-animal interactions, Balearics, islands, lizard, endemic, seeds, germination, plant invasions, conservation, *Podarcis lilfordi*.

Resumen

Se ha estudiado el efecto de la lagartija balear *Podarcis lilfordi* sobre la germinación de *Lycopersicon esculentum* (Solanaceae), en condiciones de laboratorio. El periodo de germinación se acortó significativamente tras la ingestión por las lagartijas, pero el porcentaje final de germinación (a los 10 días) no difirió entre las semi-

[1*] *Estación Biológica y de Cultura Científica de Sanaüja, Museo Nacional de Ciencias Naturales, Agencia Estatal Consejo Superior de Investigaciones Científicas (CSIC). Ap. Correos nº 35 • 25280 Solsona, Lleida, Spain. email: castilla.aurora@gmail.com; castilla@ebd.csic.es*

[2] *Estación Biológica de Doñana, Agencia Estatal Consejo Superior de Investigaciones Científicas (CSIC). C/ Americo Vespucio s/n • 41092 Sevilla, Spain. email: castilla@ebd.csic.es*

llas consumidas (91 %) y las no ingeridas (98 %). La amplitud de las fluctuaciones diarias de temperatura a las que fueron expuestas las semillas tuvo un efecto significativo sobre la duración de la germinación, pero no sobre su porcentaje final. Las pequeñas fluctuaciones diarias de temperatura (± 3,5 °C) redujeron el tiempo de germinación, comparadas con las fluctuaciones mayores (± 5,7 °C). Puesto que *P. lilfordi* mejora la germinación de *L. esculentum*, esta lagartija se puede considerar como un eficiente dispersor de la planta. Por último, se discute si los dispersores de semillas podrían ser agentes potenciales de la introducción de plantas invasoras asociados con las actividades humanas.

• Key words: interacciones planta-animal, Baleares, islas, lagartijas, endemismos, semillas, germinación, plantas invasoras, conservación, *Podarcis lilfordi*.

Laburpena

Balearetako sugandilak, *Podarcis lilfordi, Lycopersicon esculentum (Solanaceae)*-ren erneketan duen eragina, laborategiko baldintzetan aztertu da. Erneketa denbora modu esanguratsuan laburtu zen sugandilek irentsi ondoren baina batazbesteko ernalketa portzentaia (10 egun igaro ondoren) antzekoa izan zen irentsitako hazien (91 %) eta irentsi gabekoen (98 %) artean. Haziei egunetan zehar jasan arazi zitzaizkien tenperatura gorabeheren zabaltasunak eragin nabaria izan zuen erneketa iraunaldian baina ez hala azkeneko portzentaian. Eguneroko tenperatura gorabehera txikiak (± 3,5 °C) erneketa denbora gutxitu zuen, gorabehera handiagoak (± 5,7 °C) ez bezala. *P. lilfordi* -k *L. esculentum*-en erneketa hobetzen duenez, sugandila hau barreiatzaile eragingarritzat hartu daiteke. Azkenik, hazien barreiatzaileak, gizakien jarduerekin lotutako landare inbaditzaileen sarbidean ahalezko agenteak izan dezaketen eztabaidatzen da.

• Gako-hitzak: landare-animali elkarreragina, Baleareak, irlak, sugandilak, endemismoak, haziak, erneketa, landare inbaditzaileak, artapena, *Podarcis lilfordi*.

Introduction

Birds and mammals (Herrera 1989, Jordano 1992) and more recently reptiles (Braun & Brooks 1987, Cobo & Andreu 1988, Cortes Figueira et al. 1994, Valido & Nogales 1994, Castilla 1999) are considered as potential dispersers of many plant species. Frugivores indeed consume plant seeds and have an effect on their germination. However, there is great variation in responses by seeds to ingestion by herbivorous within the same plant genus or even within a single species. One of the topics necessary to understand the ecological and evolutionary aspects of plant-animal interactions, is whether seeds of different plant species respond similarly to ingestion by the same frugivore species (Traveset 1998).

It is expected that seed germination in closely related plant species would be similarly affected by the same species of vertebrate (Traveset 1998). In this study I examined the effect of the lizard *P. lilfordi* on germination performance of the Solanaceae plant *Lycopersicon esculentum*. The main objective was to compare the results of this study with those on the effect by the same lizard species on seed coat sculpture (Castilla 1999) and on germination performance (Castilla & De Ridder 1998, Castilla 2000) of the Solanaceae plant *Withania frutescens*. I also discuss the potential of legitimate dispersers as dispersal agents of invasive plants through the intervention of human activities.

MATERIAL AND METHODS

In May 1998 I captured 5 adult lizards (*Podarcis lilfordi*, snout-vent length: 59 - 67 mm, mass: 5 - 8 g) in the island of Cabrera (Cabrera National Park, Balearics, Mediterranean), and transported them to the laboratory of Functional Morphology at the University of Antwerp (Belgium). Lizards were kept in 2 terraria (50 x 40 cm) that were placed in a temperature-light controlled room (day temperature: 32-35 °C; night temperature: ca. 20-25 °C). Lizards were fed with seeds of tomato (*Lycopersicon esculentum*). Meal-worms and vitamin-enriched water were continuously available ad libitum. Terraria were inspected every 3 h to collect lizard faeces, which were subsequently examined for the presence of excreted seeds. All defecated seeds were stored in paper bags at room temperature (ca. 22 °C) during a maximum of 5 days before the start of the germination experiment.

On July 1998, 53 ingested and 53 non ingested (i.e., control) seeds were placed in Petri dishes (10 cm diameter) on a filter paper immersed in sterile distilled water. From 6 to 10 randomly selected seeds (halve ingested and halve control) were placed in each dish, and 10 dishes (= replicates) were used for each treatment. The dishes were placed in a controlled light and temperature room. Light regime consisted of 16 h of white fluorescent light and 8 h of darkness. Ambient temperature was monitored throughout the experiment at 15 min intervals with temperature data loggers (Stowaway, Onset Computer Corporation, Idaho, USA). The mean ± 1 SE of the daily average temperatures was 27.7 ± 0.1 °C. The mean amplitude of the daily temperature fluctuations was 5.7 ± 0.1 °C.

An additional sample of 60 control seeds collected from a different tomato, were placed in 6 dishes and germinated in a room having the same light conditions and average temperatures as described above. However, the mean amplitude of daily temperature fluctuation was smaller (3.5 ± 0.1 °C).

Individual seeds were inspected twice a day until all seeds had germinated. Germination time was defined as the time elapsed between the start of the experiment and the emergence of the radicle from the seed. Emerging seedlings were removed from the dish when the cotyledon and hypocotyl were visible.

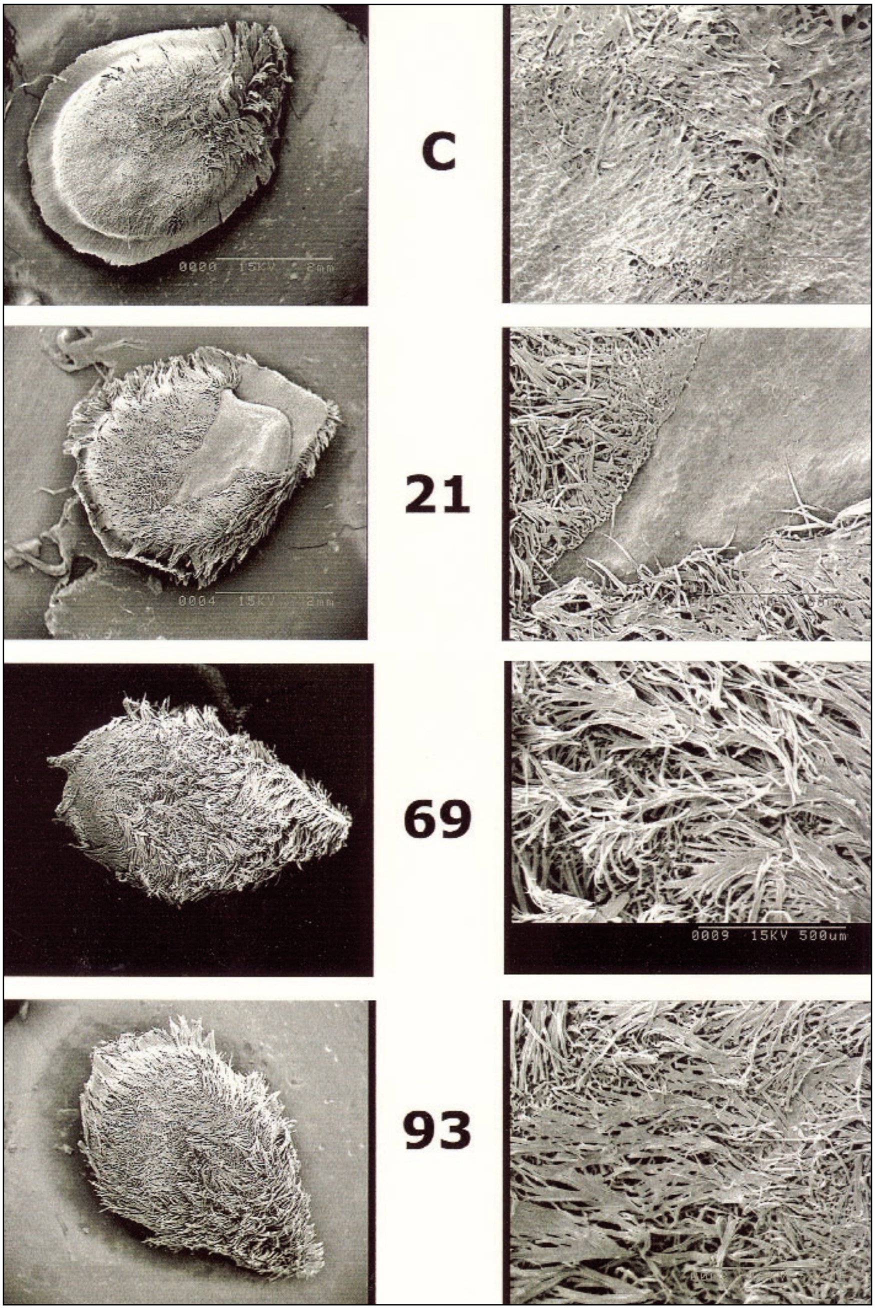

Figure 1.- Micrographs of seed coats of *Lycopersicon esculentum* that were non-ingested (control) (c), and seeds eaten by lizards that were retained in their guts during different time (hours). Photographs magnified x 20 (left) and x 100 (right).

Seed coats of 4 randomly selected seeds were washed in 70% ethanol in an ultrasound chamber during 15 minutes, then gold-coated (200-300 Amstrongs) in a vacuum (Polarom E- 5400 SEM coating system), photographed and compared (Fig. 1).

Results

The lizard *P. lilfordi* retained the tomato seeds in their guts for periods of 21 to 96 hours. Seed coat sculpture of digested seeds was abraded compared to not-ingested seeds (Fig. 1). The time to germination of *L. esculentum* seeds varied from 44 hours to 10 days, and the variability was comparable between treatments (Fig. 2). The distribution of germination time differed significantly between ingested and control seeds (Kolmogorov-Smirnov two-sample test: D = 0.284, P < 0.05). Germination was faster in ingested than uningested seeds (Fig. 2). The final percentage of germination after10 days did not differ between ingested (91 %) and non-ingested (98 %) seeds (Chi^2 = 0.84, df = 1, P > 0.30) (Fig. 2). The remaining seeds (4 ingested and 1 control) failed to germinate after 2 more weeks and were infected by fungi.

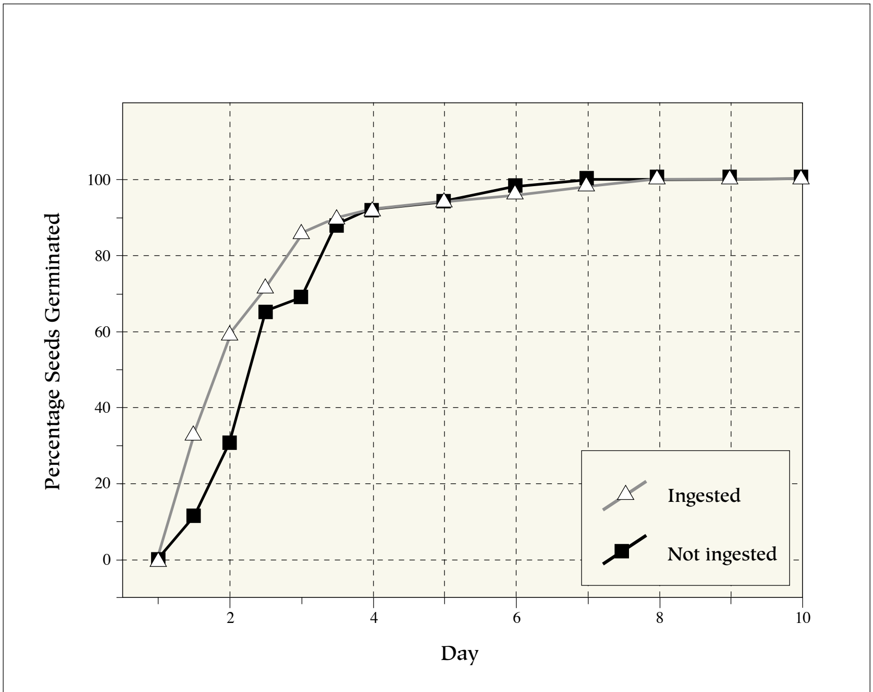

Figure 2. Cumulative percentage of *Lycopersicon esculentum* seeds that germinated at different times, for seeds that were retained in the lizard guts and for non-ingested (control) seeds.

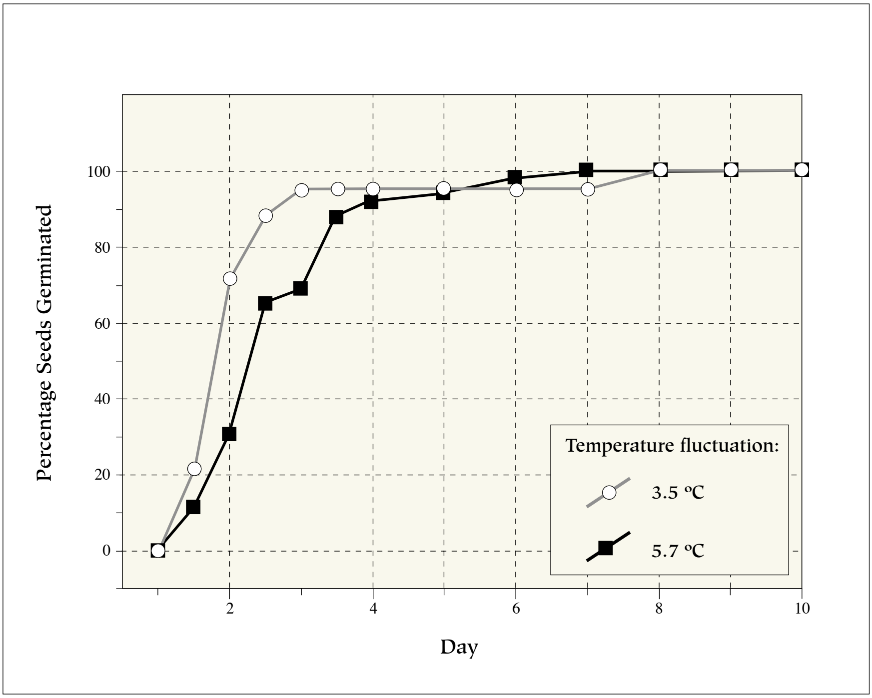

Figure 3. - Cumulative percentage of *Lycopersicon esculentum* control seeds that germinated under different temperature fluctuations.

Temperature regime was an important factor affecting germination. A small mean daily temperature fluctuations (3.5 °C), compared to a larger one (5.7 °C), reduced germination time (Kolmogorov-Smirnov two-sample test: $D = 0.409$, $P < 0.01$) but not the final percentage of germination ($Chi^2 = 1.14$, $df = 1$, $P > 0.20$) (Fig. 3).

En un caso, uno de los individuos capturados para su anillamiento (captura 06.08.2004, ver para más detalles Tab. I) presentaba anilla de remite extranjero (Museo de París). Este ejemplar se anilló en una región del NW de Francia, el 01.08.2004 (713 km en 5 días, 142,6 km/día).

Asimismo, todas las citas se registraron en la Ribera, al S de Navarra (al S de 42°30' N), excepto la cita de Cirauqui (42°40' N), a unos 25 km de Pamplona en dirección NE.

Discussion

Effect of treatment on germination

The results of this study indicate that the lizard *P. lilfordi* has a positive effect on germination time of *L. esculentum* (i.e., germination was faster in ingested than in uningested seeds). However, I did not detect an effect of ingestion on the final percentage of germination (i.e., the percentage of germination was similar in ingested and not-ingested seeds). Similar results were obtained for the Solanacea plant *Withania frutescens* with the same 5 individual lizards (Castilla 2000) or with lizards from a different population (Castilla & De Ridder 1998). Therefore, the lizard *P. lilfordi* has similar effects on germination performance of this two Solanaceae plants, despite differences in seed size (diameter of *L. esculentum* seeds: ca. 1 mm; *W. frutescens* seeds: 4-5 mm), and seed coat thickness (see photographs in Castilla 1999, present study). Seeds of both plant species were retained in the lizards guts for approximately the same time (*L. esculentum*: 21-96 hours, *W. frutescens*: 18-92 hours), despite they are rather different in size and seed coat thickness. Also, the time to germination differed considerably between species. Most *L. esculentum* seeds germinated in less than 3 days (maximum of ten days), while *W. frutescens* seeds germinated in a median time of two months (maximum of 5 months) (Castilla & De Rider 1998).

To my knowledge, the effect of frugivores on germination of *L. esculentum* seeds has been only tested with the Galapagos giant tortoise (*Testudo elephantopus*) (Rick & Bowman 1961). Similar to my results, these authors also found a positive effect of tortoise ingestion on the time of germination of *L. esculentum*, and most of their tomato seeds also germinated in 2 days (maximum of 11 days).

In contrast to my findings here, the lizard *Gallotia gallotia* from the Canary Islands reduces germination time of seeds of the Solanaceae *Whitania aristata*, but has no effect on the Solanaceae *Lycium intrincatum* (Valido & Nogales 1994, Nogales et al. 1998). Similar examples can be found with birds (Barnea et al. 1990). Differences in seed morphology, as well as in the digestive fluids of lizards, the time seed are retained, the type of food ingested along with the seeds, etc, may be responsible for differences in the effect of lizards on germination of closely related plants.

Effect of temperature on germination performance

The effect of temperature on germination performance was examined here only in control seeds that were collected from two different tomato plants. At similar mean temperatures, a small amplitude of daily temperature fluctuations reduced germination time. Thus, a difference of two degrees in the amplitude of temperature fluctuations had an effect on germination. A significant effect of temperature regime on germination was also found in *W. frutescens*, but in a different direction. Similar mean temperatures, but a larger amplitude of daily fluctuating temperatures accelerated germination and increased the percentage of seed germination of *W. frutescens* (Castilla & De Rider 1998).

Temperature is considered one of the most important environmental factors regulating germination timing and velocity (Probert 1992). The results here give support to this view and indicate the importance of different temperature regimes for embryo development in plant species.

Can legitimate dispersers indirectly promote plant invasions?

Most studies of plant-animal interactions focus on the benefit that plants get from herbivores or document the damage they produce to seeds and flowers. However, the immediate positive effect that vertebrate dispersers have on germination performance of plants may turn into a long term negative effect, if the plants consumed and dispersed by the herbivores are invaders or alien plants in a given habitat (see Rejmánek 1989).

The tomato plant is actively consumed by some lizards (e.g. *Lacerta lepida* in the Spanish mainland, own obs; *Gallotia galloti* in the Canary islands, Pérez-Mellado et al. 1999). In some archipelagos (e.g. Balearics, Columbretes, Canaries), lizards are commonly fed with tomato, either in baited traps for scientific purposes or to attract them to tourist visitors of Nature Reserves (A. Valido, V. Pérez-Mellado, com pers, and own obs.). The tomato plant, contrarily to other Solanaceae (e.g. *Solanum nigrum*, *S. dulcamara*, *S. sarachoides*), is not considered as an invasive plant (Thompson et al. 1995). However, other invasive plants (e.g. *Opuntia* sp, Williamson 1996) can be consumed by lizards in the same manner as described before. Because Cactaceae plants (e.g. *Opuntia dillenii*, *Melocactus violaceous*) can be dispersed by lizards (e.g. *Gallotia galloti*, *Tropidurus torquatus*) (Valido & Nogales 1994, Cortes Figueira et al. 1994), the use of them in baited traps can constitute a potential risk for introducing alien plants.

Many insular lizards of different genera (*Anolis*, *Gallotia, Podarcis*) consume fruits (Castilla & Bauwens 1991, Castilla 1999, Herrel et al. 2004, Lazell 1997, Pérez-Mellado & Corti 1993, Valido & Nogales 1994, Sáez & Traveset 1995), and this kind of activities may cause undesirable results. Thus, to prevent possible introductions, it should be recommended not to transport non-native fruits from one island to another for any purpose, and to use seedless fruits (e.g. removing seeds by hand or using can fruits) for trapping activities.

Feeding animals by residents and tourists in insular Nature Reserves may contribute to the same problem as described before. Because human activities (even if indirectly) may cause the introduction of alien or invasive plants, this type of activities should be prevented.

Acknowledgements

I thank the responsible of Cabrera National Park and J. Mayol for providing permission to collect the endemic lizard, the military commanders to provide facilities in the island and Dirk Bauwens for constructive comments. Laboratory climatic chambers were provided by the Research Group of Plant Physiology (Prof. J.P. Verbelen) and of Functional Morphology (Prof. F. De Vree) at the University of Antwerp (UA). Micrographs were made at the laboratory of Microscopy (Dr. F. Hierro, University of Balearics, Mallorca) and processed by Pepelu (Universidad Autónoma of Madrid). This work was supported by the Project DGICYT, PB97-1174 (to A. Traveset, IMEDEA-CSIC), the Project MEC CGL2005-00391/ BOS (to J. Martín & P. López, MNCN-CSIC), and by a contract "Ramón and Cajal" from the Spanish National Science Foundation (CSIC, Ministerio de Ciencia e Innovación).

BIBLIOGRAPHY

- BARNEA, A., YOM-TOV, Y. & FRIEDMAN, J. 1990. Differential germination of two closely related species of Solanum in response to bird ingestion. *Oikos* 57: 222-228.
- BRAUN, J. & BROOKS, G. R. JR. 1987. Box turtles (*Terrapene carolina*) as potential agents for seed dispersal. *Am. Midl. Nat.* 117: 312-318.
- CASTILLA, A. M. 1999. *Podarcis lilfordi* from the Balearic Islands as a potential disperser of the rare Mediterranean plant *Withania frutescens*. *Acta Oecologica* 20: 103-107.
- CASTILLA, A. M. 2000. Does passage time through lizard (*Podarcis lilfordi*) guts affect germination performance of the pant *Withania frutescens*? *Acta Oecologica* 21: 119-124.
- CASTILLA, A. M. & BAUWENS, D. 1991. Observations on the natural history, present status, and conservation of the insular lizard *Podarcis hispanica atrata* on the Columbretes archipelago, Spain. *Biol. Conserv.* 58: 69-84.
- CASTILLA, A. M. & RIDDER, F. 1998. The effect of lizard gut-passage on germination performance in the Solanacea plant *Withania frutescens*. 5th Benelux Congress of Zoology, Phylogeny and Biodiversity. University of Gent, Belgium.
- COBO. M. & ANDREU, A. C. 1988. Seed consumption and dispersal by the spur-thighed tortoise *Testudo graeca*. *Oikos* 51: 267-273.
- CORTES-FIGUEIRA, J. E., VASCONCELLOS-NETO, J., GARCÍA, M. A. & TEXEIRA DE SOUZA, A. L. 1994. Saurocory in *Melocactus violaceous* (Cactaceae). *Biotropica* 26: 295-301.
- HERREL A, VANHOOYDONCK B & VAN DAMME R. 2004. Omnivory in lacertid lizards:adaptive evolution or constraint ? *Journal of Evolutionary Biology* 17:974-984.
- HERRERA, C. M. 1989. Frugivory and seed dispersal by carnivorous mammals, and associated fruits characteristics, in undisturbed Mediterranean habitats. *Oikos* 55: 250-262.
- JORDANO, P. 1992. Fruits and frugivory, pp. 105-156. In Fenner, M. (eds.). *Seeds, the ecology of regeneration in plant communities*. Commonwealth Agricultural Bureau International, Wallingford.
- LAZELL, J. 1997. *Anolis cristatellus* Wileyae. Frugivory. *Herp. Rev.* 28: 150.
- NOGALES, M., DELGADO, J. D. & MEDINA, F. M. 1998. Shrikes, lizards and *Lycium intricatum* (Solanaceae) fruits: a case of indirect seed dispersal on an oceanic island (Alegranza, Canary Islands). *J. Ecol.* 86: 866-871.

- Pérez-Mellado, V. & Corti, C. 1993. Dietary adaptations and herbivory in lacertid lizards of the genus *Podarcis* from western Mediterranean islands (Reptilia: Sauria). *Bonn.Zool. Beitr.* 44: 193-220.
- Pérez-Mellado, V., Romero-Beviá, M., Ortega, F., Martín-García, S., Perera, A., López-Vicente, M. & Galache, C. 1999. El uso de los recursos tróficos en *Gallotia simonyi* (Sauria, Lacertidae) de la isla de El Hierro (Islas Canarias). *Monogr. Herpetol.* 4: 63-83.
- Probert, R. J. 1992. The role of temperature in germination ecophysiology, pp. 285-325. In Fenner, M. (eds.). *Seeds. The ecology of regeneration in plant communities.* CAB International United Kingdom, UK.
- Rejmánek, M. 1989. Invasibility of plant communities, In Drake, J. A, Mooney, H. A., di Castri, F., Groves, R. H., Kruger, F. J., Rejmánek, M. & Williamson, M. H. (eds.). *Biological invasions: a global perspective.* Wiley, Chichester.
- Rick, C. M. & Bowman, R. I. 1961. Galápagos, tomatoes and tortoises. *Evolution* 15: 407-417.
- Sáez.E & Traveset, A. 1995. Fruit and nectar feeding by *Podarcis lilfordi* (Lacertidae) on Cabrera archipelago (Balearic islands). *Herp. Review* 26: 121-123.
- Thompson, K., Hodgson, J. G., & Rich, C. G. 1995. Native and alien invasive plants: more of the same? *Ecography* 18: 390-402.
- Traveset, A. 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review, pp. 151-190. In Edwards, P. J. (eds.). *Perspectives in plant ecology, evolution and systematics.* Vol. 1/2. Gustav Fisher Verlag, Zurich.
- Valido, A. & Nogales, M. 1994. Frugivory and seed dispersal by the lizard *Gallotia galloti* (Lacertidae) in a xeric habitat of the Canary Islands. *Oikos* 70: 403-411.
- Williamson, M. 1996. Invasions. *Ecography* 22: 5-12.

- Fecha de recepción/Date of reception: 01/06/2008
- Fecha de aceptación/ Date of acceptance: 01/07/2008