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Breakage of mutualisms by exotic species: the case of *Cneorum tricoccon* L. in the Balearic Islands (Western Mediterranean Sea)

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Abstract

Aim In this study we tested the hypothesis that the dispersal success (estimated here as fruit removal rate) of a native shrub species living in the Balearic Archipelago, *Cneorum tricoccon* L. (*Cneoraceae*), has decreased significantly in those islands where endemic lizards of the genus *Podarcis* have disappeared. These lizards acted as the main seed dispersers of the plant and became extinct after the introduction of carnivores. At least one of these carnivores, the pine marten (*Martes martes* L.), is also an important frugivore, consuming the fruits and dispersing the seeds of *C. tricoccon* and thus allowing the comparison of fruit removal rates between the two groups of vertebrates (lizards and mammals). We further tested the possibility that lizards (in particular, *P. pityusensis* Boscà) could be exerting selection on seed size.

Methods In seven populations from four islands, we monitored fruit removal by either lizards or mammals. The fruits of *C. tricoccon* do not drop after ripening, remaining attached to the branches for long periods if not removed. In order to test whether lizards might be exerting selection on seed size, we compared seed diameter and weight between defecated and uningested (collected directly from plants) seeds for each of the populations.

Results Fruits were removed in significantly greater proportions in those populations where lizards are still present. Data showed that in two of the examined populations in the Pityusic islands, defecated seeds were lighter and smaller than controls suggesting that lizards selected fruits of smaller size than the average of the population.

Main conclusions The introduction of carnivores in the Balearics has led to important changes in the population dynamics of many native species. In the larger islands (Mallorca and Menorca), carnivores seemed to have caused the extinction of endemic lizards who acted as the only dispersers of some plants such as *C. tricoccon*. Pine martens, in particular, are in turn frugivorous and thus can 'replace' to some extent the 'lost' seed dispersers. We hypothesize that besides having decreased fruit removal rates in this shrub, these 'new' dispersers have modified considerably the distribution of the plant on Mallorca island, as the fossil record shows that lizards lived at low altitudes (< 500 m a.s.l.) and the plant can be currently found up to 1000 m a.s.l. Furthermore, preliminary data suggest that lizards might be exerting a selective pressure on seed size. If this is true, this pressure might have been released – or counteracted if carnivores select for fruit size as well – after the extinction of lizards from some islands, which would have important ecological consequences for the plant.

Keywords
Plant–lizard interactions, seed dispersal, frugivory, *Cneorum tricoccon*, *Podarcis*, carnivorous mammals, Balearic Islands, western Mediterranean.

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INTRODUCTION

Island floras are particularly vulnerable to invasion of exotic biota because of the intrinsic characteristics of islands (Vitousek *et al.*, 1995). Oceanic islands, in particular, like Hawaii, New Zealand or Galapagos, have many examples of the negative impact that alien species can have on native plant communities (e.g. Smith, 1985; Brockie *et al.*, 1988; Holzapfel *et al.*, 2001; Jäger *et al.*, 2001). Abundant evidence also exists for continental or para-oceanic islands (those that are biologically similar to oceanic ones have been connected to the continent in the past; Alcover *et al.*, 1998) indicating that the introduction of exotic species into a habitat may have deleterious effects on the native flora (Di Castri *et al.*, 1990; Jeanmonod, 1998; Vilà & Muñoz, 1999). Much less information is available, however, on the effect that those introductions have on species interactions, and specifically, on plant–animal mutualisms. Some studies have shown the detrimental effect on plant–pollinator interactions (e.g. Aizen & Feinsinger, 1994a,b; Vaughton, 1996; Cox & Elmqvist, 2000; Holzapfel *et al.*, 2002) whereas a few others have described a plant–seed disperser disruption (e.g. Cox, 1983; Bond & Slingsby, 1984; Traveset, 1995a; Christian, 2001) that may lead to dramatic declines in population sizes of the plants involved in such interactions (Traveset, 2002; A. Traveset & N. Riera, unpublished data) and even to shifts in plant community composition (Christian, 2001; Meehan *et al.*). Moreover, the consequences of these mutualism–disruptions may not only be ecological but also evolutionary (e.g. Valido, 1999). When the introduced exotic species is an animal, the possibility exists that it 'replaces', to a certain degree, the animal partner of the disrupted interaction (for instance, by pollinating or dispersing the same plants that the native animal species pollinates or disperses). This has been found, for instance, in Hawaii with the introduction of *Zosterops japonica* (Temminck et Schlegel), a nectarivorous bird that replaces the unique but currently extinct pollinators of native plants such as *Freycinetia arborea* Gaud. (Cox, 1983). Another example has been reported from Madagascar, where the introduced *Apis mellifera* L. depletes nectar resources from endemic trees, thus competing with native nectar feeding birds and insects (Hansen *et al.*, 2002). In such cases, the plant population is not expected to be as negatively influenced as it would be if the plant had been absolutely deprived of its animal mutualists. These 'not-so-unfavourable' introductions of exotic species in natural systems, however, occur probably in only a few occasions.

A particular type of plant–animal interaction which might be importantly threatened by the introduction of new species into a habitat, and mainly described from island ecosystems (see review in Lord *et al.*, 2002), is seed dispersal by lizards (saurochory). Studies examining the tightness of this mutualism are rare (but see Whitaker, 1987; Traveset, 1995a, 2002; Valido, 1999; Wotton, 2000; Lord & Marshall, 2002; A. Traveset & N. Riera, unpublished data) and, thus, for most systems, we do not have the information needed to predict the consequences of a disruption in such an interaction. In the present study we examine the consequences of a plant–lizard mutualism disruption for the dispersal success (estimated here as the rate of fruit removal) of a plant living in the Balearic Archipelago (western Mediterranean Sea), *Cneorum tricoccon* L. (Cneoraceae). The endemic lizards of the genus *Podarcis* that acted as its main (probably the only) dispersers became extinct from the large islands of the Archipelago (Mallorca and Menorca) after the introduction of carnivorous mammals, mainly pine martens (*Martes martes* L.), genets (*Genetta genetta* L.) and weasels (*Mustela nivalis* L.). Pine martens and genets, however, are in turn good consumers of fruits, acting as legitimate seed dispersers of a wide variety of plant species, including *C. tricoccon* (Traveset, 1995a; Clevenger, 1996). The degree to which such carnivores substitute for lizards as seed dispersers on those islands is unknown, although the seed shadow they produce is probably quite different from that generated by lizards as their foraging behaviour and ranges are quite different. There is no fossil evidence that other native animals, either mammals or birds, acted as dispersers of *C. tricoccon* in the past (Traveset, 1995a). A tight plant–lizard interaction has also been described in the Canary Islands, between the only other member of the family Cneoraceae, *Neochamaelea pulverulenta* (Vent.) Erdtm., and endemic lizards of the genus *Gallotia* (Valido, 1999).

By looking at a number of populations of *C. tricoccon* on different islands and islets of the Balearics, with and without carnivores, our specific aim in the present work is to test the hypothesis that the disappearance of lizards from Mallorca and Menorca has had an important quantitative effect on the dispersal success of this plant. In addition, we present preliminary data on the possible selective pressure that lizards may exert on fruit/seed size on those islands/islets where they still persist.

METHODS

Study species

Cneorum tricoccon is a perennial shrub often shorter than 1 m (although some individuals can reach *c.* 2 m) that has a disjunct distribution in the western Mediterranean basin. It is common in the Balearic Islands, having been recorded on fourteen islands/islets (Bonafé, 1979; Alomar & Bibiloni, unpubl. data), and it has small populations in the south-eastern Iberian Peninsula, south-eastern France, south-western Sardinia and north-western Italy (Bolòs, 1958) (Fig. 1). On the continent, it usually inhabits coastal maquis or shrublands, usually in calcareous soils (Blanca *et al.*, 1999). In the Balearic Islands, the species has also colonized the interior of the large islands, and it is often found in the understorey of oak forests (*Quercus ilex* L.) up to an altitude of around 1000 m a.s.l. (Traveset, 1995a, 2002). The species belongs to a Mediterranean flora that evolved during the early Tertiary under tropical conditions (Raven, 1973; Axelrod, 1975; Herrera, 1985) and it thus represents a relict species. Its pollination system has already been examined (Traveset, 1995b). The fruit consists of three cocci (locules of a

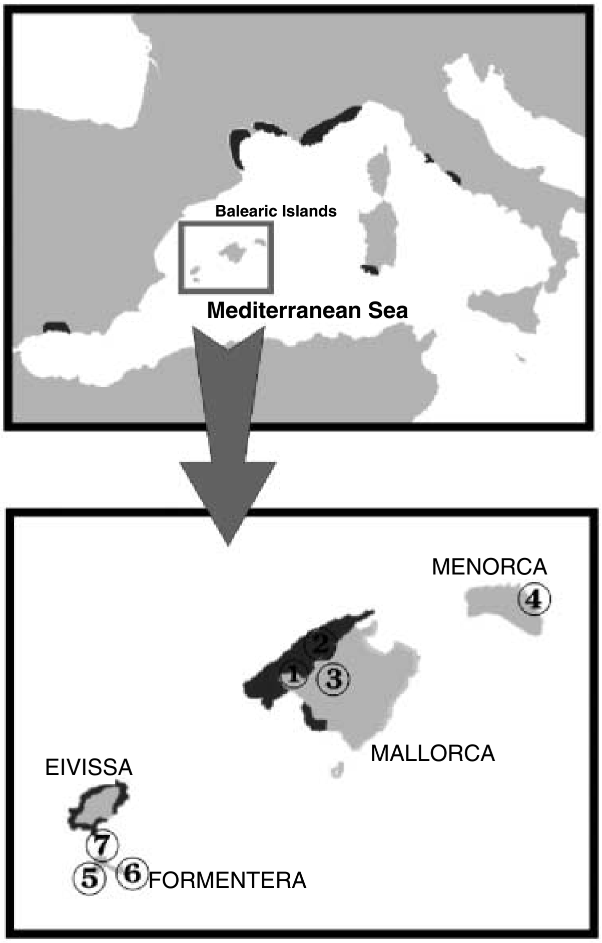

Figure 1 Map of the western Mediterranean Sea showing the distribution of *Cneorum tricoccon*. Below, the Balearic Islands on which the studied populations are indicated. 1: S'Arboçar, 2: Lluc, 3: Puntiró, 4: Sa Mesquida, 5: Cap de Barbaria, 6: La Mola, 7: S'Espalmador.

syncarpous ovary) that easily fall apart into three pieces, each of which contains two one-seeded compartments. Occasionally, two or four cocci are observed. Mature fruits are first seen by mid March, although the ripening peak is usually in April, and fruits are sometimes seen until June. Each coccus is a red drupe when ripe that measures, on average 5.7 ± 0.054 mm (SD) ($n = 315$) in cross diameter and weighs 0.139 ± 0.003 g (SD) ($n = 315$). Fruits that are not consumed can remain on the plant for long periods (often more than a year); they either dry up or are infested by a fungus that turns them black (Traveset, 1995b). *Cneorum* seeds have been observed outside ant nests which suggests that these insects probably act as secondary dispersers (N. Torres, pers. comm.).

A study of the population age structure of *C. tricoccon* in the south-eastern Iberian Peninsula has revealed that most individuals are more than 50-year old and that there is low seedling recruitment, suggesting a low level of seed dispersal (Blanca *et al*., 1999). The seed dispersal agents in those populations are unknown, although preliminary observations suggest that a species of lizard (*Lacerta lepida* Daudin) might consume the fruits and disperse the seeds (J. Hódar, pers. com.). In the Balearics, seedling recruitment is generally low, being highest in the Pitysiuc islands (Eivissa, Formentera and surrounding islets) (N. Riera, unpubl. data). We do not know yet whether recruitment is limited more by the number of dispersed seeds than by the number of microsites suitable for germination and growth (an ongoing study is being carried out to assess this).

There are two species of *Podarcis* (Lacertidae) in the Balearic Islands: *Podarcis lilfordi* (Günter, 1874) and *P. pityusensis* (Boscà, 1883). *Podarcis lilfordi* is an endemic lizard from Mallorca, Menorca and surrounding islets. Currently, it is present only on surrounding islets, as it disappeared from Mallorca and Menorca because of the introduction of carnivorous mammals (Mayol, 1985). *Podarcis pityusensis* is endemic to the Pityusic islands; it can be found in all the different habitats of the islands, being scarce in the extensive pinewoods but very common in the scrub vegetation and walls. Of all lacertid species in the Mediterranean region, the two endemic lizards of the Balearics are among the few that include a large proportion (up to 70% in some localities in the case of *P. pityusensis*; N. Riera, unpubl.data) of plant material in their diet. The highest proportion of plant matter corresponds to fleshy fruits. Herbivory in these two species of *Podarcis* can be explained in terms of resource availability, but may also be the result of historical influences. The isolation of these lizards took place during the Messinian period (about 5 Myr ago), which was characterized by very dry climatic conditions (Alcover & Mayol, 1981). The Balearic Archipelago was at this time in the centre of a saline steppe that acted as a filter for colonization of the area (Alcover & Mayol, 1981). It is therefore feasible that there was strong natural selection for lizards with high trophic adaptability to adopt a herbivorous diet.

Carnivorous mammals have been introduced by man since Roman times in the Balearics (Alcover, 1980). Only pine martens and genets can be considered as important frugivores, as they include important amounts of fleshy fruits in their diets. On Mallorca, the frequency of occurrence by season of fleshy fruits found in pine marten faeces ranges from 50 to 76.4% (Clevenger, 1996 and references therein). On Menorca, in contrast, a larger subspecies (*M. martes* sbp. *minoricensis*) includes much smaller proportions of plant material in its diet (Clevenger, 1993a), what has been attributed to (1) the lack of interespecific competition with genets, absent in this island, and/or to (2) the temporal food (fruits and other resources) availability and abundance on each island (Clevenger, 1996). Pine martens occupy nearly 50% of both Mallorca and Menorca, mainly in pine and oak forests, although they also inhabit scrublands and riparian forests. They are not present in any of the other surrounding islands. Genets are less important frugivores (Clevenger, 1996), and the fact that they defecate in latrines and in sites usually unsuitable for germination and seedling growth makes those animals inefficient seed dispersers (Traveset, 1995a, 2002). Genets are present only in Mallorca, Eivissa and Cabrera islands.

Birds do not consume the fruits of *C. tricoccon* (Traveset, 1995a), probably because of the high amount of secondary compounds (mainly tannins) in their pulp (Traveset, unpublished data).

Fruit removal

We chose seven populations of *C. tricoccon* from the Balearics to monitor fruit removal by frugivores, either lizards or carnivores: three populations from Mallorca island (Finca S'Arboçar, Lluc and Puntiró) along the Serra de Tramuntana mountain chain which runs from north to south-west, one population (the only remaining) from Menorca (Sa Mesquida), and the other three from the Pityusic islands, two from Formentera island (Cap de Barbaria and La Mola) and one from S'Espalmador islet (Fig. 1). During June of 2001, we labelled three branches and recorded the number of fruits on them from a minimum of ten individuals in each population from Mallorca and Menorca and from a minimum of twenty-five individuals from the Pityusics (in these populations, the entire number of fruits per plant were counted because of the small fruit crop produced this year). A month later, all labelled plants were checked and the number of remaining (already drying) fruits was recorded. This species does not drop the fruits after ripening and they remain attached to the branches if not removed (dry fruits can be observed on the plant even a year later); thus, we are quite confident that the missing fruits we recorded had been removed by animals.

Fruit selection

We wanted to test the possibility that lizards (in particular, *P. pityusensis*) could be exerting selection on seed size (highly correlated with fruit size) of *C. tricoccon*, as found by Valido (1999) in *N. pulverulenta* in the Canary Islands. From 6 March to 23 May 2000, we collected fleshy fruits from *C. tricoccon* shrubs in Cap de Barbaria ($n = 55$ shrubs), La Mola ($n = 30$) and S'Espalmador ($n = 20$) and faeces of *P. pityusensis* bearing *C. tricoccon* seeds from those three populations ($n = 100$, 131 and 26 scats, respectively). Only fresh droppings were harvested and placed individually in small vials. For each population and for the two treatments (ingested vs. uningested), we measured seed weight and diameter to the nearest 0.1 mg and 0.01 mm, respectively). In 2001, these measurements were repeated but this year, mainly because of the low fruit production compared with 2000, we could obtain enough seeds for both treatments only from La Mola, which were gathered during June. We additionally compared seeds of both treatments from an island on the western coast of Mallorca (Dragonera island); here we collected both lizard scats and *Cneorum* fruits directly from plants on 22 June, 2001.

Data analysis

A series of one-way analysis of variance (ANOVAS) were performed to test for differences in fruit removal rates among populations and to compare seed measurements between treatments. The angular transformation was used to normalize the proportions. All means are accompanied with their standard errors unless otherwise indicated.

RESULTS

Highly significant differences were found in percentage of fruit removal when comparing all seven populations ($F_{6,145} = 38.15$, $P < 0.001$). Removal was highest in the populations where lizards are present (Fig. 2), although considerable variation existed among the populations in Mallorca (from 15% in Puntiró to 80% in Lluc). When we grouped populations according to lizard presence or absence, the difference in percentage fruit removal per plant also showed to be highly significant ($86.9 \pm 2.5\%$ vs. $42.9 \pm 4.3\%$, respectively; $F_{1,150} = 96.41$, $P < 0.01$).

Our preliminary results of fruit selection by lizards indicate that these animals might exert a selective pressure on seed size, at least in some populations and in some years (for all populations, the size of each coccus is highly correlated with the size of the seed it contains; $r = 0.731$, $P < 0.0001$; $n = 265$). Data from 2000 showed that in two of the three examined populations, defecated seeds were lighter and smaller than controls collected from plants (Table 1), suggesting that lizards selected fruits of smaller size than the average of the population. In 2001, however, defecated seeds from La Mola were significantly heavier and larger than controls ($F_{1,111} = 51.76$ and 35.07, respectively; $P < 0.001$). This contradictory result is attributed to the very dry conditions in 2001 in the Pityusic islands, with almost no rainfall. This dry year, fruits from all plants were significantly smaller than in 2000 [0.020 ± 0.001 g for seed weight and 2.98 ± 0.035 mm for seed diameter ($n = 49$); $F_{1,104} = 255.146$ and 36.387, respectively, $P < 0.0001$, and see Table 1] and lizards seemed to choose the larger ones, although they were

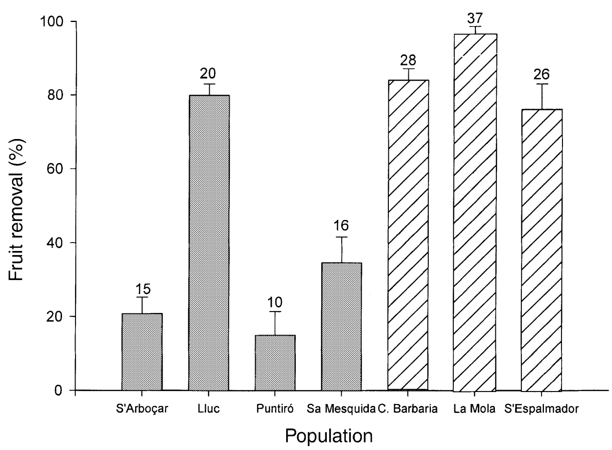

Figure 2 Percentage fruit removal of *C. tricoccon* by either carnivores (in the Mallorcan and Menorcan populations; dark columns) or lizards (in the Pityusic islands; slashed columns). Data from 2001. Numbers and bars on each column indicate sample sizes and standard error of the mean, respectively.

Table 1 Seed dimensions (mean and standard error) of the two treatments (defecated by *Podarcis pityusensis* and uningested, control seeds) from each of the three studied populations

	Seed diameter (mm)			Seed weight (g)		
Population	Controls	Defecated	*F*-values	Controls	Defecated	*F*-values
Cap Barbaria	4.79 ± 0.04 (60)	4.78 ± 0.04 (174)	$F_{1,232} = 0.02$ ns	0.049 ± 0.001 (60)	0.046 ± 0.003 (174)	$F_{1,232} = 0.34$ ns
La Mola	4.91 ± 0.07 (50)	4.64 ± 0.05 (89)	$F_{1,137} = 9.94$*	0.059 ± 0.002 (50)	0.043 ± 0.001 (89)	$F_{1,137} = 53.15$*
S'Espalmador	4.51 ± 0.06 (25)	4.17 ± 0.09 (23)	$F_{1,46} = 9.46$*	0.051 ± 0.002 (25)	0.031 ± 0.002 (23)	$F_{1,46} = 54.52$*

Data are from 2000. Numbers in parentheses represent sample sizes. *$P < 0.01$.

still smaller than those selected in 2000 [0.031 ± 0.001 g for seed weight and 3.41 ± 0.06 mm for seed diameter ($n = 64$)]. When comparing dimensions from lizard-defecated and control seeds from Dragonera island, we found no significant differences neither for seed weight ($F_{1,124} = 0.002$, $P = 0.97$) nor diameter ($F_{1,124} = 0.01$, $P = 0.91$).

DISCUSSION

The significantly greater number of fruits remaining undispersed in those populations where lizards are extinct support the hypothesis that the dispersal success of *C. tricoccon* has decreased after the introduction of carnivores in those islands. Although such carnivores – especially pine martens – consume the fruits of this shrub, they seem to be less effective, at least quantitatively, than lizards. Data gathered in previous years (1992–94) from two populations in Mallorca (Puntiró and Cap Blanc) and in Cabrera, another island south of Mallorca where lizards persist, support these results: mean fruit removal in the Mallorcan populations was between 44 and 66%, respectively, whereas it ranged from 92 to 99% in Cabrera (Traveset, 1995a). We cannot discard the possibility, however, that such intense fruit removals by lizards take place only in small islands, with less diverse and abundant food resources than in Mallorca or Menorca. It may well be that removal of *Cneorum* fruits from these two large islands has always been rather low or moderate and that the introduction of frugivorous carnivores has influenced more the distribution than the abundance of this shrub. Nonetheless, the fact that lizards are territorial, the easy accessibility of fruits to them, and the low number of species in the habitat fruiting at the time *C. tricoccon* does, lead us to think that fruit removal in Mallorca and Menorca was higher when lizards were present in these islands than nowadays.

In Menorca, the only remnant population of *C. tricoccon* consists of about fifty individuals. The fossil record indicates that this species was more widespread in this island than it is now (A. Traveset, J. Quintana and J.A. Alcover, unpublished data) and we attribute this to the disappearance of lizards and to the current low seed dispersal success. Although pine martens are present, they include a much lower proportion of fruits in their diet than in Mallorca, presumably because of the absence of competition for animal food with other carnivores (Clevenger, 1996). Further studies on the different factors that may limit plant population growth, such as seedling recruitment and survival, are needed to assess the probability of extinction of *C. tricoccon* on Menorca.

In the Pityusic Islands, the only disperser of *C. tricoccon* is *P. pityusensis*, except in some Eivissa populations where genets are present (Alcover, 1984; Clevenger, 1996). The density of lizards on these islands is quite high (Salvador, 1984) and they are present on all islands/islets where *C. tricoccon* is found (see Table 1 in Traveset, 2002). When fruits of this plant are ripe, lizards can commonly be seen climbing the shrubs to reach them. Further examination of the fate of the defecated seeds is required to determine how efficient such lizards are in dispersing them to sites favourable for germination and establishment.

The tropical conditions under which *C. tricoccon* lived in the past were probably more favourable than current conditions and, thus, it is reasonable to think that the plant has modified its physiognomy considerably. Nowadays, individuals more than 1 m tall are usually found in the most humid habitats, often under oaks. In coastal zones and in islets, shrubs are often shorter than 0.5 m and appear much less leafy. The total production of fruits varies greatly among individuals and populations and is highly correlated with plant size (Traveset, 1995a; N. Riera, unpublished data). Hence, it is likely that plants produce much less fruits now than they did in the humid conditions that prevailed in the past.

It also seems very probable that the plant has modified its distribution (moving to higher altitudes) as carnivores have begun dispersing the seeds. According to the fossil record, *P. lilfordi* (endemic to Mallorca, Menorca and adjacent islets) did not live above *c.* 500 m a.s.l. (Alcover *et al.*, 1981). Currently, it is common to find *C. tricoccon* above an altitude of 1000 m in the Serra de Tramuntana mountain chain (Fig. 1). Pine martens, and also genets, are known to have extensive home ranges (up to 900 ha in the case of pine marten males), their foraging areas include a wide variety of habitats (Clevenger, 1993b) and, at least pine martens, have been located at altitudes over 1000 m (G. Alomar, pers. comm.). Therefore, they are likely to be the main animals responsible for the current widespread distribution of *C. tricoccon*.

The different *C. tricoccon* populations found on islands/islets where lizards are the only seed dispersers represent an ideal system to test whether these reptiles can exert an important selective pressure on fruit and seed size, as has been suggested for *N. pulverulenta* in the Canary Islands (Valido, 1999) and for different species native to New Zealand that are also dispersed by lizards (Lord & Marshall, 2002). The data gathered in 2000 from two populations of the Pityusic islands do suggest that lizards are selecting small fruits. The snout–vent length of lizards varies significantly among populations (ranging from 58.0 to 85.4 mm; Salvador, 1984) and this variation might well be correlated with that of fruit and seed size. Unfortunately, we do not have data from enough populations to test this hypothesis at present, although this is the goal of an ongoing study. If lizards do exert a selective pressure on seed size, we may hypothesize that this pressure has been released in those islands where pine martens are now the main dispersers (i.e. in Mallorca and Menorca); such pressure may be actually counteracted by a possible selection of large fruits by the carnivores. Seed size in *C. tricoccon* is probably influenced by a number of factors. Preliminary data from continental populations of this species (from Málaga, in southern Iberian Peninsula) show, for instance, that larger seeds germinate in greater proportions than the smaller ones (Blanca *et al.*, 1999). Further work is therefore required to determine the causes and consequences of the variation in fruit and seed size that we currently observe in this plant.

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