

## Seed dispersal of *Cneorum tricoccon* L. (Cneoraceae) by lizards and mammals in the Balearic islands

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### Abstract

The seed dispersal system of *Cneorum tricoccon*, a shrub with a distribution restricted to the western Mediterranean area, was examined in the Balearic Islands. The endemic lizards, *Podarcis lilfordi* and *Podarcis pityusensis* (Lacertidae), consume important quantities of fruits of the plant, acting as legitimate dispersers on the islands where they are present. Where lizards have become extinct, like in Mallorca and Menorca islands, introduced carnivorous mammals (pine martens, *Martes martes*, and spotted genets, *Genetta genetta*) play now the role of seed dispersers and have probably influenced present-day distribution and abundance patterns of the plant. Lizards usually remove all mature fruits from the plants whereas a large proportion of fruit remains undispersed in areas where carnivores are the only dispersers. It is hypothesized that lizards have for a long time been the major dispersers of this Mediterranean relict plant which evolved under tropical conditions during the early Tertiary, as it has probably happened with its relative *Neochamaelea pulverulenta* in the Canary Islands.

**Keywords:** Cneoraceae, *Cneorum tricoccon*, vertebrate seed dispersal, *Podarcis*, *Martes martes*, *Genetta genetta*, Balearic islands, western Mediterranean.

### Résumé

La dispersion des graines de *Cneorum tricoccon*, un arbuste dont la distribution est limitée à la Méditerranée occidentale, a été étudiée sur les îles Baléares. Les lézards endémiques, *Podarcis lilfordi* et *Podarcis pityusensis* (Lacertidae), mangent une quantité importante de fruits, agissant comme disperseurs légitimes de cette plante, sur les îles où ils sont présents. Là où ces lézards se sont éteints, comme à Majorque et Minorque, des mammifères carnivores introduits (martres, *Martes martes*, et genettes, *Genetta genetta*) jouent alors le rôle de disperseurs de graines. Les lézards extraient habituellement tous les fruits mûrs des plantes, mais une grande proportion de fruits n'est pas dispersée dans les zones où les carnivores sont les seuls disperseurs.

On fait l'hypothèse que les lézards ont longtemps été les principaux disperseurs de cette plante relique méditerranéenne qui a évolué sous des conditions tropicales au début de l'ère tertiaire, comme cela a été le cas de son congénère *Neochamaelea pulverulenta* aux îles Canaries.

## INTRODUCTION

*Cneorum tricoccon* L. (Rosidae, Cneoraceae) is a small evergreen shrub, with a restricted distribution to the western Mediterranean (HEYWOOD, 1985). Together with *Neochamaelea pulverulenta* (included in the genus *Cneorum* before the revision by HANSEN & SUNDING (1993)), an endemic to the Canary Islands, they are the only members of the family. A third species, *C. trimerum*, had been reported from Cuba (CHODAT, 1921) but it appears to be a synonym of *C. tricoccon* (LOBREAU-CALLEN & JÉRÉMIE, 1986). *C. tricoccon* is moderately common in all the Balearic Islands and is present at some localities of the eastern and southern Iberian Peninsula, southeastern France, Sardinia, Liguria and Toscana, being usually found in the coastal maquis (BOLÓS, 1958; BONAFÉ, 1979).

The seed dispersal ecology has not been previously studied for either species, although anecdotal data on the animals that consume the fruits of these shrubs are found in some studies. ALCOVER (1984) and CLEVINGER (1995a, b) report the spotted genet, *Genetta genetta*, as a fruit consumer of *C. tricoccon* in Cabrera island (Balearic Archipelago) whereas MORENO *et al.* (1988) and CLEVINGER (1995a, b) find seeds of this species in the scats of pine marten, *Martes martes*, in Mallorca and Menorca islands. For *N. pulverulenta*, VALIDO & NOGALES (1994) recently reported that seeds of this species pass intact through the stomach of *Gallotia galloti*, a lizard endemic to the Canary Islands.

The goal of the present study was to examine with more detail who are the main fruit consumers of *C. tricoccon* in the Balearic Islands, whether they act as legitimate dispersers and what is the dispersal success of the plant. The composition of the vertebrate fauna varies among islands, so it was expected that the disperser assemblage would also vary among them. The fruits of *C. tricoccon* are fleshy, red when ripe and of the size of those typically consumed by birds; thus, even though there are no reports of avian fruit consumption on this plant, the possibility that birds eat the berries and act as dispersers was also investigated.

## STUDY AREA AND PLANT

The study was carried out in the islands of Cabrera and Mallorca, and additional observations were made in Eivissa and Formentera. These islands have a Mediterranean climate, with hot and dry summers and mild winters in which temperatures rarely are below 0°C. The common vegetation in which *C. tricoccon* is found, usually in patches, is scrubland mainly dominated by *Pistacia lentiscus*, *Phillyrea* spp., *Olea europaea*, *Juniperus phoenicea*, *Euphorbia dendroides*, *Erica multiflora*, *Rosmarinus officinalis* and *Cistus* spp. A brief description of the vegetation of all the Balearic Islands can be found in BONNER (1989).

*Cneorum tricoccon* is an andromonoecious, insect-pollinated species (TRAVERSE, 1995). It has a long flowering period that lasts from the end of October through April (though sometimes flowers are still present in June). The ovaries of the hermaphrodite flowers grow continuously and reach full size several weeks after anthesis. The fruit consists of three cocci (locules of a syncarpous ovary) that fall easily 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 are sometimes seen until June. Each coccus is a red drupe when ripe that measures, on average,  $4.6 \pm 0.4$  mm (s.d.) ( $n=25$ ) in cross diameter. Fruits that are not consumed can remain on the plant for a long period (often more than a year); they either dry up or are infested by a fungus that gives them a black color (TRAVESET, 1995). *Cneorum* seeds have been observed outside ant nests which suggests that these insects probably act as secondary dispersers (N. TORRES, pers. comm.).

## METHODS

A total of 31 individuals of *C. tricoccon* were marked in Cabrera island during the fruiting season of 1992 and monitored until mid July. The same individuals (except one that died) plus 20 supplementary ones were also monitored during the fruiting period of 1993. In the island of Mallorca, I examined fruit removal in two southern populations: one in Cap Blanc (UTM 31T DD 78 7 63 5) during 1993 (25 individuals), and the other in Pontiró (UTM 31T DD 81 8 82 7) during 1994 ( $n=20$  individuals).

Fruit crops of the monitored plants were recorded in all three populations. The number of fruits not dispersed (dried or with fungi) was recorded from the Cabrera population on July of 1992 and 1993. In Mallorca, undispersed fruits were counted in Cap Blanc on October 1993 and in Pontiró on October 1994.

To test whether seeds remain viable after passing through the animals' digestive tract, a bioindicator, TTC (2, 3, 5 triphenyl tetrazolium chloride), that stains viable embryos was used (HEYDECKER, 1968).

Scats of vertebrates (birds, mammals and lizards) were collected in Mallorca and Cabrera in the areas where *C. tricoccon* is found, and were examined to determine the presence of seeds of this species. A total of 30 faeces of pine marten were found and collected at Serra de Na Burguesa (Serra de Tramuntana, Mallorca). In Cabrera, 60 lizard scats were examined at the site where the plant is found. The faeces of genets both in Mallorca and Cabrera have been examined by CLEVINGER (1995a, b) for a study on the feeding ecology of this carnivore. Consumption of *Cneorum* fruits by birds was examined in Cabrera island during the spring of 1992, both directly (making observations on the plants for about a total of 10 hours) and indirectly (by examining over a hundred scats of frugivorous birds, caught by means of mist nets placed near the *Cneorum* population).

Additional observations of fruit consumers were made in the Pityusic islands, Eivissa and Formentera, during May of 1994.

## RESULTS

Table I summarizes the assemblages of dispersers of *C. tricoccon* by island, showing also the degree of reliance on this plant.

In Cabrera island, the only consumers of *C. tricoccon* fruits are the endemic lizard *Podarcis lilfordi* (Günther, 1874) (Lacertidae) and the spotted genet (*Genetta genetta*). During the fruiting period, lizards are often observed climbing the shrubs to reach the ripe or ripening fruits and swallowing the cocci one by one. Occasionally, they bite the pulp without removing the fruits, thus not acting as legitimate dispersers (SÁEZ & TRAVESET, 1995). Of the 60 lizard scats examined in the area, 57 (95.0%) bore *C. tricoccon* seeds, usually two or three per scat. The seeds showed to be viable after passing through the animal's guts. Genets, on the other hand, do not seem to be important dispersers of *Cneorum* given the low (<2%) frequency with

TABLE I. – Dispersers of *Cneorum tricoccon* in the different Balearic Islands and their reliance on the plant (W: weak; XX: strong). The numbers indicate the references where *Cneorum* seeds are reported to be found in the faeces of each species. The dash indicates that the species is not present in the island. Both the spotted genet and the pine marten are not native to the Balearics but introduced by man (see text).

Island	<i>G. genetta</i>	<i>M. martes</i>	<i>P. lilfordi</i>	<i>P. pityusensis</i>
Mallorca	X <sup>1,2</sup>	XX <sup>1,2,3,4</sup>	Extinct	–
Menorca	–	XX <sup>3,4</sup>	Extinct	–
Cabrera	X <sup>1,3</sup>	–	XX <sup>5</sup>	–
Eivissa	X <sup>1</sup>	–	–	XX <sup>5</sup>
Formentera	–	–	–	XX <sup>5</sup>

References: <sup>1</sup> ALCOVER (1984); <sup>2</sup> ALCOVER (1988); <sup>3</sup> CLEVINGER (1995a, b); <sup>4</sup> MORENO *et al.* (1988); <sup>5</sup> present study.

which seeds of this species appear in their faeces (CLEVINGER, 1995b). Moreover, the fact that this carnivore usually defecates in latrines, which may be located inside caves or in other places not suitable for seed germination, decreases the probability that it acts as an efficient seed disperser.

Birds do not appear to consume the fruits of *C. tricoccon*. During the direct observations, not a single bird was seen visiting the plants, although birds were observed eating the fruits of other species available at the time such as *Pistacia lentiscus* (which still bore ripe fruits from the last winter) and *Rhamnus ludovici-salvatoris* (TRAVERSE, 1992). Furthermore, none of the examined scats of frugivorous birds (*Sylvia atricapilla*, *S. melanocephala*, *S. borin*, *Erithacus rubecula*, *Phoenicurus phoenicurus*, *P. ochruros*, *Turdus philomelos*, *Sturnus vulgaris* and *Fringilla coelebs*) contained *Cneorum* seeds.

In Mallorca island, where lizards went extinct a long time ago (see discussion's section), the current main seed dispersers are pine martens (not present in Cabrera; ALCOVER, 1988) and spotted genets. In Serra de Na Burguesa (southern Serra de Tramuntana), where *C. tricoccon* is quite common, all examined faeces of pine marten, found mainly along trails, had abundant (up to 176) seeds of this plant. Those seeds appear to be viable with the TTC's test. *Cneorum* seeds have also been reported from genet faeces of Mallorca (ALCOVER, 1984), although it is unknown how important this species may be as a seed disperser in this island. Based on the number of faeces found, genets are less common than pine martens in Mallorca (CLEVINGER, 1995a), so probably the former is a less important seed disperser than the latter.

In the Pityusic islands, *Podarcis pityusensis* Boscá 1883 is quite common and appears to play a major role dispersing the seeds of *C. tricoccon*. Lizards are commonly observed climbing the shrubs and removing the ripe fruits which can often be near a meter from the ground. Genets are present in Eivissa and scats of this carnivore with *Cneorum* seeds are reported by ALCOVER (1984) and by CLEVINGER (1995a, b). In the smallest Formentera, there are neither genets nor pine martens (ALCOVER, 1988), and the only disperser is thus the endemic lizard (table I).

Table II shows the data on fruit removal that took place in the populations studied during the different years. Removal differed significantly among sites ( $F_{2,123} = 75.8$ ,  $P = 0.0001$ ), being greater in Cabrera than in Mallorca. The number of fruits remaining undispersed was significantly greater in Pontiró (more than half the initial number of fruits) than in Cap Blanc (Scheffé's test). Fruit removal in

TABLE II. – Removal of *C. tricocon* fruits in the study sites. Lizards consume most fruits in Cabrera island, whereas removal in Mallorca (Cap Blanc and Pontiró) is done only by mammals (pine martens and spotted genets).

Population and year	Initial No. fruits/plant Median (range; n)	% of fruits removed Mean $\pm$ std (n)
Cabrera		
1992	90 (17-299; 31)	99.3 $\pm$ 1.5 (31)
1993	34 (3-213; 51)	92.2 $\pm$ 13.2 (51)
Cap Blanc		
1993	29 (4-222; 25)	65.9 $\pm$ 31.8 (25)
Pontiró		
1994	307 (52-817; 20)	43.9 $\pm$ 22.7 (20)

the two Mallorcan populations was even somewhat overestimated since number of fruits remaining was recorded in October and a fraction of them might have already been dropped and lost in the ground.

There was a significant correlation between plant fecundity and absolute number of fruits removed in all populations (Pearson correlations:  $r = .99$  and  $r = .90$ , for Cabrera in 1992 and in 1993, respectively;  $r = .94$  for Cap Blanc, and  $r = .77$  for Pontiró, all  $P = 0.0001$ ). However, the proportion of the crop that was removed was not associated with the number of fruits produced ( $P \gg 0.05$ ). The only exception was Cabrera, where in 1992 more fecund plants had a lower proportion of the fruits removed (Spearman correlation:  $r_s = -0.57$ ,  $P < 0.001$ ,  $n = 31$ ). As table II shows, plant fecundity was several times greater in one of the Mallorcan populations, Pontiró, than in Cap Blanc or than in Cabrera. This is due to the greater size of the plants at Pontiró (unpubl. dat.) which is located at a higher elevation (200 m) than the other populations (almost at sea level). It appears that *C. tricocon* grows better at higher altitudes and at more humid sites. The most vigorous individuals, reaching over 1 m in height, have been seen at Serra de Tramuntana, over 500 m elevation (pers. obs.). Also, in all islands, plants located in the shade tend to be larger and more leafy than those exposed to sun.

## DISCUSSION

The seed disperser assemblage of *Cneorum tricocon* in the Balearics varies among islands depending upon the frugivorous vertebrates present in them. In Cabrera, and in the islets surrounding it, the endemic lizard *P. lilfordi* appears to be the major disperser of this plant, consuming large amounts of fruits and defecating viable seeds in places where they can germinate and grow. Possibly due to a limitation of food resources, the fruits are eaten by lizards soon after ripening and sometimes even before completing maturation. Likewise, in the Pityusic islands the endemic *P. pityusensis* is apparently the most important disperser of *C. tricocon*.

In Mallorca, with no lizards currently present, mature fruits remain on the plant much longer due to the lower removal by carnivorous mammals – pine martens and spotted genets –, and a large proportion of such fruits (which can be up to 50%

of the crop) is never dispersed, drying off or rotting on the plant. In this island, and also in Menorca, the lizard disappeared after 250 A.D., coinciding with the introduction, by man, of predators such as weasels and snakes (SANDERS, 1984). Pine martens and spotted genets were probably introduced later, although there is no definite evidence for this (ALCOVER, pers. comm.). Nowadays, pine martens occupy about 50% of the whole island territory, both in Mallorca and in Menorca, and the highest densities are found in the upland/open pine forests (CLEVINGER, 1993, 1994). Protection of this species during the last 25 years has enabled it to recover throughout most of the forested habitats on both islands from which almost went extinct due to hunting (CLEVINGER, 1993). It is reasonable to think, thus, that the distribution and abundance of *C. tricoccon* in these two islands has been importantly influenced by the population dynamics of such carnivore.

A strong spatial variation in the dispersal success of *C. tricoccon* was found depending upon the fauna present in the area where the plant is located. In the island of Cabrera, where most or all fruits are consumed, more fecund plants probably have a greater probability of dispersing more seeds successfully, having a higher fitness than plants with a low fecundity. In Mallorca, in contrast, fruit removal is much lower (sometimes being almost nul), and small individuals may have a greater proportion of seeds dispersed than larger, more fecund ones, possibly due to differences in carnivore densities among sites.

The current species of mammals found in the Balearic Islands have all been introduced by man (ALCOVER, 1988), therefore the mutualistic interaction *Cneorum*-lizards is much older than the *Cneorum*-mammals one. The mammals that inhabited Mallorca and Menorca in the past were not fruit-consumers (*Nesiotites*, a species of shrew) or would have acted more as seed predators than as seed dispersers: a species of rodent, *Eliomys*, and a bovid with a rodent-like dentition, *Myotragus* (ALCOVER *et al.*, 1981). The latter, however, might have actually acted as a disperser if the hard seeds of *Cneorum* survived its teeth and the pass through its digestive system. In the Pityusic Islands, where fossil seeds of *Cneorum* have been found (at Cova de Ca Na Reia, Eivissa; ALCOVER, pers. comm.), there were no mammals during the Upper Pleistocene and the Holocene (ALCOVER, 1988), so they could not be dispersers of this plant.

*Cneorum tricoccon* belongs to a group of plants of the Mediterranean flora selected out of a diverse array of species which evolved under a warm, summer-rain, tropical climate in the Tertiary environments (MÜLLER, 1933; RAVEN, 1973; AXELROD, 1975; HERRERA, 1985). Its unusual phenology and the fact that it grows better in humid and shady sites may actually be attributed to its tropical relict condition. *C. tricoccon* was already present in the early Tertiary (MÜLLER, 1933:402); hence, it is possible that the disperser assemblage has changed along time. Although in the present scenario birds do not consume its fruits, the possibility exists that the plant was, in the past, dispersed by some components of the tropical African avifauna – birds such as those in the families Coliidae, Musophagidae, or Trogonidae, among others (CRACRAFT, 1973) – which was present in Europe during the mid-Tertiary period and was probably in contact with *Cneorum*. The plant, however, has coexisted with lizards for a long period of time and, so, the mutualistic interaction is probably a very old one. The oldest fossil record of lizards in the Balearics dates back to the Upper Miocene (ALCOVER *et al.*, 1981; MOYÀ-SOLÀ *et al.*, 1984; AGUSTÍ & MOYÀ-SOLÀ, 1990). A parallel case, which

supports the possibility of a very old plant-lizard interaction, is found in the other member of the family, *N. pulverulenta*, in the Canary Islands. This plant is also dispersed by the endemic lacertids *Gallotia galloti* (VALIDO & NOGALES, 1994) and *G. stehlini* (VALIDO & NOGALES, pers. comm.) and, curiously, no birds have ever been observed consuming the fruits of this plant either (VALIDO & NOGALES, pers. com.). Unfortunately, no information is available on the dispersers of *C. tricoccon* in the other areas where it lives.

The plant-disperser mutualistic interaction in the *Cneorum* system seems to be an ancient one. The fossil seeds found in Eivissa appear with the same size and structure as those produced today (pers. obs.) which indicates that the selective pressures acting on fruit traits have probably been very weak for quite a long time. Such slow evolutionary change in those traits might be explained, at least partially, by a constancy in the vertebrate dispersal, assuming lizards have been the main dispersers of *Cneorum* for a long period of time. Evidence supporting the constancy, over geological time, of dispersal traits of other Mediterranean vertebrate-dispersed taxa with a Tertiary origin has been reported for other species in the genera *Pistacia laurus* and *Osyris* (HERRERA, 1984, 1986, 1988).

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