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Original article

Responses of mammal dispersers to fruit availability: Rowan (*Sorbus aucuparia*) and carnivores in mountain habitats of northern Spain

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ABSTRACT

Despite the well known fact that carnivore mammals are important fruit consumers and legitimate seed dispersers in temperate habitats, little is known about their quantitative responses to fruit availability. Here we show the results of two studies conducted at two different temporal and spatial scales, that were intended to assess the response of pine martens (*Martes martes*) and red foxes (*Vulpes vulpes*) to variations in the supply of rowan (*Sorbus aucuparia*) fruits in the Cantabrian Range (northern Iberia). First, we studied the association between fruit availability and the importance of rowan fruit in the diet of carnivores during a period of 11 consecutive years. This was accomplished by comparing fruit-crop size in 54 trees and the analysis of faecal contents in a sample of 863 faeces. Secondly, we assessed the consumption of fruits by these two species underneath the canopy of 20 rowan trees along 10 consecutive days. In the first study, the diet of martens and foxes consistently tracked interannual variations in rowan fruit availability, despite large fluctuations in fruit yield that included three mast years of heavy rowanberry crops and three non-fruiting years. For both carnivores total crop size was correlated with the frequency of occurrence and the proportion of rowan by volume in faeces. The second study suggested that carnivores feeding on fallen fruit tended to visit the trees that exhibited a higher density of fruits under the canopy. Thus, carnivores apparently choose to feed on high-density patches of fruit, which in turn were located underneath the canopy of the trees that produced the larger crops. Our results stress the need to pay proper attention to the role of carnivores as seed dispersers, in order to disentangle the evolutionary and ecological outcomes of plant-animal interactions in mixed-dispersed plants.

1. Introduction

Carnivorous mammals are known to consume fleshy fruits and to disperse their seeds after gut passage. The important role of bears, procyonids, canids and mustelids, as consumers and dispersers of fleshy-fruit plants is arguably a characteristic feature of many temperate habitats, thus contrasting with tropical environments where apparently monkeys, rodents, bats and large herbivores predominate in mammal frugivore assemblages (Willson, 1991). Carnivores participate in the dispersal of 40% and 89% of the fleshy-fruit plants occurring in south-eastern Spain and southern France respectively (Herrera, 1989; Debussche and Isenmann, 1989; see also Rosalino and Santos-Reis, 2009), about 50% of the fleshy-fruit plants of cool-temperate deciduous forest habitats in Japan (Koike et al., 2008) and as much as 69% of the fleshy-fruit plant genera in North America (Willson, 1993). Nonetheless, while just a few fleshy-fruit species in temperate floras are consumed only by mammals, many are consumed by birds and mammals, thus having mixed-dispersal strategies (Herrera, 1989; Debussche and Isenmann, 1989; Willson, 1993). Despite this, the ecological and evolutionary interpretations of seed dispersal mutualisms in non-tropical habitats lay, to a great extent, on the study of avian dispersal agents (see Herrera, 1989 and references therein) whereas mammals are often ignored. Vertebrate-dispersed plant systems must be studied in their whole complexity with regard to all potential selective agents on plant traits (Herrera, 1986). In species consumed by birds and mammals, failing to account for one group of dispersers can be highly misleading as relevant differences are to be expected in the quality and quantity components of disperser effectiveness (*sensu* Schupp, 1993) due to the morphological, behavioural and ecological differences that exist between the two groups. Some features such as the number of seeds dispersed by visit, seed treatment, seed transit time, seed

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rain patterns and seed deposition quality (Herrera, 1989; Debussche and Isenmann, 1989; Hickey et al., 1999; Traveset et al., 2001; Traveset and Verdú, 2002; Clark et al., 2005; Jordano et al., 2007) have been shown to be different in birds and mammals, while many others still remain unexplored. From an adaptive point of view, fruit tracking is a key issue in seed dispersal mutualisms. When fruit supply has little effect on the ecology of frugivores or when the variation in frugivore numbers has little effect on the reproduction of plants, selection pressures are severely constrained, thus limiting frugivore and plant specialization (Wheelwright, 1988; Levey and Benkman, 1999; Herrera, 2002) while emphasizing the nonequilibrial nature of the system (*sensu* Herrera, 1998a). Inconsistencies in the temporal or spatial coupling of plants and frugivores are likely to affect the evolutionary potential of the interaction (Jordano, 1993; García and Ortíz-Pulido, 2004). Therefore, fruit tracking is particularly relevant in temperate habitats, where substantial temporal and spatial variation in fruit abundance is widespread (Herrera, 2002). Several descriptive and experimental studies have succeeded in finding evidence of numerical and functional responses by avian frugivores to fruit-resource abundance (e.g.: Moegenburg and Levey, 2003; Hampe, 2008; Guitián and Munilla, 2008, and references therein), although this issue still remains controversial (see Herrera, 1998a). With respect to mammals, several studies have suggested demographic responses in association with fruit-resource availability (e.g.: Mattson et al., 1991; Fleming, 1992; Noyce and Garshelis, 1997; Ganesh and Davidar, 1999; Feer et al., 2001; Lambert et al., 2006; Nakagawa et al., 2007) and diet studies have shown that seasonal variation in fruit consumption is quite common in frugivorous carnivores (e.g.: Jedrzejewski et al., 1993; Ferrari and Weber, 1995; Pandolfi et al., 1996; Bermejo and Guitián, 1996; Martinoli et al., 2001; Otani, 2002; Baltrunaite, 2002; Schaumann and Heinken, 2002). However, explicit and quantitative covariation with fruit supply (i.e.: spatio-temporal variation in fruit abundance is linked to changes in the diet of carnivores and/or carnivore abundance) is yet to be addressed in carnivores and other fruit eating mammals (but see Moegenburg and Levey, 2003, for a likely response of fruit eating mammals to fruit supply).

Here, we study the response of carnivores to rowan, *Sorbus aucuparia*, fruit abundance at two spatio-temporal scales. The rowan is a masting tree mainly dispersed by birds and carnivores (e.g.: Pulliainen, 1978; Guitián et al., 2000; Jedrzejewski et al., 1993) which exhibits large synchronic interannual variations in fruit production (i.e., masting behaviour). First, we investigated the long-term dietary response of carnivores to the supra-annual variation in rowan fruit production over 11 years (long-term perspective at the landscape scale). Secondly, we investigated the response of carnivores to variations in fruit production among trees over a 10-day period (short-term perspective at the scale of individuals). To confront the idea of fruit-resource tracking by frugivorous carnivores, the following two questions were specifically addressed: (1) Is the interannual variation in rowan fruit consumption by frugivorous carnivores linked to the supply of rowan fruit? (2) Do frugivorous carnivores respond to differences in rowan fruit availability among individual trees?

2. Methods

2.1. Study area

The study was conducted at two localities (sites 1 and 2) of the Cantabrian Range (northern Spain). Site 1 was located in the upper Esla river basin, between the mountain passes of Tarna and Ventaniella (León province, 1400–1600 m a.s.l.). Here the landscape comprises large areas of beech (*Fagus sylvatica*) woodland, *Genista* scrubland, *Erica* and *Calluna* heathland and extensive pastures. Site 2 was located at Ortigoso (Cervantes, Lugo province, 1500 m a.s.l.) 140 km to the west of site 1. The natural vegetation consists of mixed deciduous woodland (mostly birch *Betula alba* and *Quercus robur* and *Quercus petraea* oaks) in a matrix of *Erica australis* heathland, together with small villages surrounded by agricultural land.

2.2. The species

The rowan (*S. aucuparia*) is a fleshy-fruiting tree commonly found in Europe north of 40° latitude. It is a mast seeding species, thus showing intermittent and synchronous production of heavy seed crops in certain years (i.e., mast years). In northern Spain it grows above 900 m a.s.l. in heathland, field hedgerows and woodland margins and gaps. The fruits are 8–9 mm in diameter and dry pulp composition is 55–80% carbohydrates, 3% lipids and 3% proteins (Guitián et al., 2000). In the Cantabrian Range the spatial distribution of rowans is extremely aggregated and the species exhibits considerable variation in fruit-crop size among years. Variations in fruit production are highly synchronic not only within populations but also between populations, at the scale of tens of kilometres (see Pías et al., 2006). At the two study sites, the main mammal consumers of rowan fruits are pine martens (*Martes martes*, Mustelidae) and red foxes (*Vulpes vulpes*, Canidae). These are the commonest carnivores in Cantabrian mountain habitats in altitudes above 1.000 m a.s.l. and fruits comprise an important part of their diets in summer and autumn (Bermejo, 1995).

2.3. Long-term tracking

Interannual variation in the importance of rowan in the diet of carnivores and fruit-crop size was measured during an 11-year period (1992–2002). Fruit production was estimated in early September, prior to fruit consumption by vertebrates and long before fruits commenced to fall to the ground, by counting the number of corymbs (infrutescences) in 54 small sized trees individually marked. In each tree, the number of fruits per corymb was calculated as the mean of 10 randomly selected corymbs. Because fruit production is highly synchronic at the landscape scale, fruit-crop size in our sample can be a reliable index of rowan fruit production over a wide area. The consumption of rowan fruit by carnivores was assessed through the analysis of the contents of faeces collected along two sampling transects. Transects ran across the rowan crop sampling area and were 5 and 6 km in length. Diet sampling was conducted in October, when rowan fruit consumption by martens and foxes was at its maximum (see Bermejo and Guitián, 1996). Sampling transects were cleared of carnivore faeces at the beginning of October and all faeces observed at the end of the month were collected for analysis. This allowed to estimate the October rate of scat deposition in all the sampling years which was expressed as number of faeces per km. In total, 863 pine marten ($n = 474$) and red fox ($n = 389$) faeces were collected. The main criteria for the identification of faeces were shape and size. Faeces that could not be properly assigned to any of the two species (10–20% of faeces) were rejected. Two measures were used to express the importance of rowan fruit in the diet of carnivores: (1) the frequency of occurrence relative to the total number of faeces collected (i.e., proportion of faeces containing rowan fruit remains) and (2) the mean proportion of rowan by volume.

2.4. Short-term tracking

Our main aim was to know if frugivorous carnivores selected trees depending on the amount of fruit available underneath their