

Honeybees Increase Fruit Set in Native Plant Species Important for Wildlife Conservation

Luis Cayuela · Sarah Ruiz-Arriaga ·
Christian P. Ozers

Received: 4 May 2010 / Accepted: 2 April 2011 / Published online: 26 April 2011
© Springer Science+Business Media, LLC 2011

Abstract Honeybee colonies are declining in some parts of the world. This may have important consequences for the pollination of crops and native plant species. In Spain, as in other parts of Europe, land abandonment has led to a decrease in the number of non professional beekeepers, which aggravates the problem of honeybee decline as a result of bee diseases. In this study, we investigated the effects of honeybees on the pollination of three native plant species in northern Spain, namely wildcherry *Prunus avium* L., hawthorn *Crataegus monogyna* Jacq., and bilberry *Vaccinium myrtillus* L. We quantified fruit set of individuals from the target species along transects established from an apiary outwards. Half the samples were bagged in a nylon mesh to avoid insect pollination. Mixed-effects models were used to test the effect of distance to the apiary on fruit set in non-bagged samples. The results showed a negative significant effect of distance from the apiary on fruit set for hawthorn and bilberry, but no significant effects were detected for wildcherry. This suggests that the use of honeybees under traditional farming practices might be a good instrument to increase fruit production of some

native plants. This may have important consequences for wildlife conservation, since fruits, and bilberries in particular, constitute an important feeding resource for endangered species, such as the brown bear *Ursus arctos* L. or the capercaillie *Tetrao urogallus cantabricus* L.

Keywords *Apis mellifera* · Bilberry · Cantabrian Mountains · Hawthorn · Pollination · *Tetrao urogallus* · *Ursus arctos* · Wildcherry

Introduction

The pollination of flowering plants by animals represents a critical ecosystem service of great value to humanity, both monetary and otherwise (Kearns and others 1998). Honeybee (*Apis mellifera* L.) is a non-native pollinator in most continents and may be detrimental for native bees and other pollinators (Roubik 1978; Schaffer and others 1983; Paton 1993; Vaughton 1996; Gross and Mackay 1998; Gross 2001; Hansen and others 2002; Thomson 2006). Even within its native European range, the species could be displacing other insects by reducing the resource base (Forup and Memmott 2005). Honeybees are however critically important for crop pollination worldwide (Watanabe 1994; Klein and others 2007), and the yields of some fruit, seed and nut crops can decrease by more than 90% without these pollinators (Southwick and Southwick 1992). Several studies have stressed the importance of honeybees for fruit and seed yields in different crops and cultivars, including sunflower *Helianthus annuus* L. (Degrandi-Hoffman and Chambers 2006), buckwheat *Fagopyrum esculentum* Moench (Goodman and others 2001; Racys and Montviliene 2005), cotton *Gossypium hirsutum* L. (Rhodes 2002), canola *Brassica napus*, L. (Manning and Boland 2000;

L. Cayuela · S. Ruiz-Arriaga
Fundación Internacional para la Restauración de Ecosistemas (FIRE), Edificio de Ciencias Ambientales, Despacho B, Campus Universitario, Universidad de Alcalá, 28871, Alcalá de Henares, Madrid, Spain

L. Cayuela (✉)
Área de Biodiversidad y Conservación, Departamento de Biología y Geología, Universidad Rey Juan Carlos, c/ Tulipán s/n, 28933 Móstoles, Madrid, Spain
e-mail: luis.cayuela@urjc.es

C. P. Ozers
Fondo para la Protección de Animales Salvajes (FAPAS), La Pereda s/n, 33509 Llanes, Asturias, Spain

Manning and Wallis 2005; Oz and others 2008), Assam lemon *Citrus limon* (L.) Burm. (Gogoi and others 2007), pear *Pyrus communis* L. (Stern and others 2007), apple *Malus domestica* Borkh. (Stern and others 2007), Japanese plum *Prunus salicina* Lundl. (Stern and others 2007), rabbiteye blueberry *Vaccinium ashei* Reade (Dedej and Delaplane 2003), and the ornamental flower *Salvia splendens* Sello (Sánchez and others 2002). Fewer studies have focused on the effects of managed honeybees on the pollination of native plants, reporting either positive effects (e.g., Gross (2001) in Australian woodlands; Chamberlain and Schlising (2008) in Californian savannas), no effects (e.g., Dupont and others (2004) in sub-alpine deserts of the Canary Islands, Spain), or even negative effects (e.g., Gross and Mackay (1998) in Australian tropical rainforests) when compared to the performance of wild pollinators.

Honeybee colonies are declining in some parts of the world (Williams and others 1991; Matheson and others 1996; Delaplane and Mayer 2000) largely owing to: (i) the spread of pests such as parasitic mites (*Varroa jacobsoni* Oudemans, *V. destructor* (Anderson & Trueman) and *Acarapis woodi* Hirst; Downey and Winston 2001; Chen and others 2004), the small hive beetle (*Aethina tumida* Murray; Evans and others 2003) and the microsporidian parasite *Nosema ceranae* n. sp. (Higes and others 2006); (ii) improper pesticide and herbicide use (Ingram and others 1996); (iii) ageing of the beekeeper population, especially in Europe and North America; and (iv) low market prices for their products and services (MacDonald and others 2000). The number of beekeepers has declined, and so has the number of colonies being kept over most of Europe (Potts and others 2010) and North America (Ellis and others 2010). Pollination has been adversely affected by this decline, and farmers have reported difficulties in obtaining services for crops such as blueberries in Maine, pome fruit in the northeastern United States and Canada, almonds in California, field cucumbers in the eastern United States and Canada, and hybrid seed production in western Canada (Kevan and Phillips 2001).

Within Europe, where the species is native, Spain holds one of the largest numbers of bee colonies (after Turkey and Romania), with some 1,800,000 hives (APISERVIC-ES, available at www.beekeeping.com/countries, accessed in September 2010). However, professional beekeeping involves only 32% of the 24,606 beekeepers currently carrying out this activity in Spain (Bulboa Cortés and Martínez Avilés 2007). This highlights the importance of apiculture as a secondary economic activity in rural areas, where it provides a supplementary income and food to beekeepers and their families, in addition to its contribution to agricultural development through crop pollination. Unfortunately, 40% of Spain's bee flock has been wiped

out in recent years, mainly due to bee diseases. This situation has been aggravated by intensification of traditional farming practices and land abandonment, especially in mountain areas (MacDonald and others 2000).

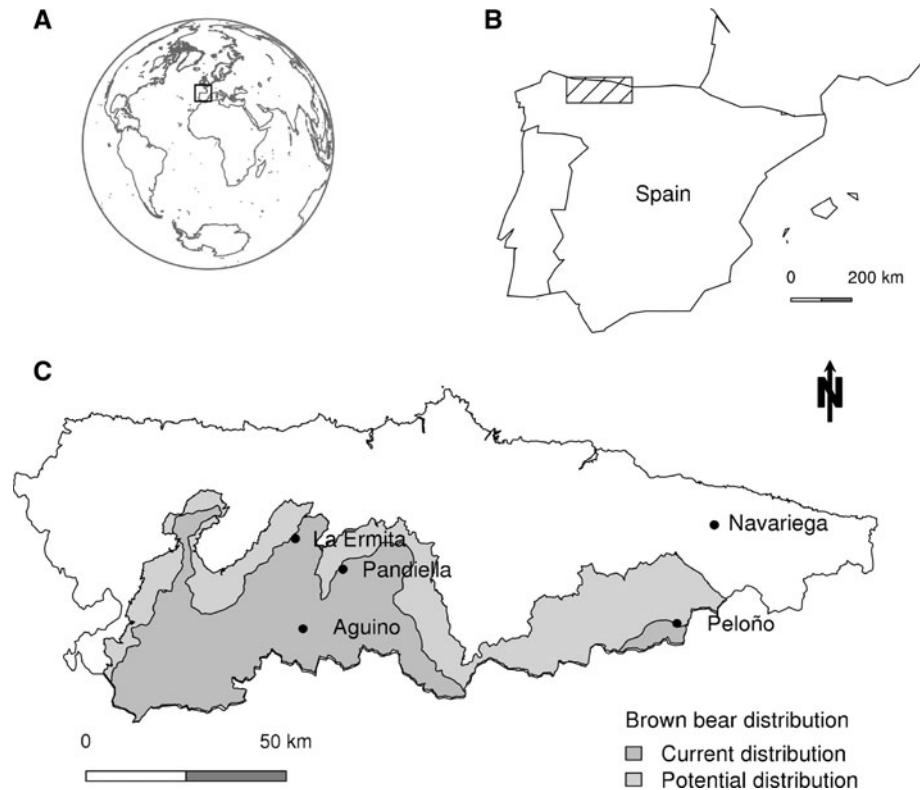
In northern Spain, adequate pollination of plants with fleshy fruits can be critical for the conservation of wildlife. Species such as the brown bear *Ursus arctos* L. (Palomero 2007) and the capercaillie *Tetrao urogallus cantabricus* L. (Storch and others 2006), which are currently in the Spanish Red List of endangered species, rely for feeding on fruits from different native plants, at least during part of the year. To date, no studies have investigated the effects of honeybees on native plant species in traditional agroecosystems, where apiculture has been a common practice for centuries (but see Gross and Mackay 1998; Gross 2001; Dupont and others 2004; Chamberlain and Schlising 2008 for some examples in natural ecosystems). The main goal of this study was to assess the influence of honeybees on fruit set of different native tree and shrub species. For this purpose, we collected data about fruit set from flowers visited by insect pollinators versus unvisited flowers at different distances from bee hives. Experimental treatments were applied to three different native plants, namely the wildcherry *Prunus avium* L., the hawthorn *Crataegus monogyna* Jacq., and the bilberry *Vaccinium myrtillus* L. We tested whether flowers of target plant species were successfully pollinated by wild pollinators as the influence of honeybees diminished at increasing distances from hives. The implications of our results for wildlife conservation are discussed in the context of the intense debate developed during recent years around the respective contributions of wild and managed pollination service components and the potential impacts of honeybees on native flora and fauna.

Material and Methods

Study Area

The Cantabrian Mountains of north-western Spain run east-west along the Atlantic coast, with a maximum altitude of 2,648 m (Fig. 1). The regional climate is a complex mixture of Atlantic, Alpine and Mediterranean influences. The proximity to the ocean and its geographic orientation result in high rainfall on north-facing slopes (average annual rainfall of 900–1900 mm) and rain shadow on southern slopes (average annual rainfall of 400–700 mm). The study area is located within the Orocantabrian province in the Eurosiberian region, on the border with the Mediterranean domain, which is dominant in the Iberian Peninsula. Twenty-five percent of the territory is covered by a natural wooded surface, mainly beech *Fagus sylvatica* L. and oak *Quercus petraea* (Matts. Liebl.) and *Q. pyrenaica* Willd, in

Fig. 1 Representation of the study area in the world (A), within Spain (B) and location of the five study sites in relation to the real and potential distribution of the brown bear (*Ursus arctos* L.). The distribution of the capercaillie (*Tetrao urogallus* L.) is not shown as it largely overlaps with the distribution of the brown bear



addition to abundant chestnut *Castanea sativa* Mill.; 2% of forest crops (*Pinus* sp. and *Eucalyptus globulus* Labill.), 8% of broom (*Genista florida* L. and *Cytisus scoparius* L.), 32% of heath (*Erica* sp.) and gorse (*Genista hispanica* L.), 23% of herbaceous plants, 3% of rocky outcrops, and 2% of sub-alpine or alpine territory, and the remaining artificial or highly modified areas. The Cantabrian mountains are also home to an important variety of animal species, including the brown bear *Ursus arctos*, cataloged as being in danger of extinction (Palomero 2007), and the capercaillie *Tetrao urogallus cantabricus*, cataloged as being of special interest in the Spanish Red List (Storch and others 2006).

The region has a long history of human settlement. Agriculture probably started in Roman times, as in much of the Mediterranean region. The current appearance of this cultural landscape is therefore the product of many centuries of interaction between humankind and the environment (Gómez-Sal 1994).

Experimental Design and Field Sampling

Sampling sites were located within or close to the range of the brown bear and/or the capercaillie, in mountain valleys where there was a single apiary and no evidence of feral honeybees in order to avoid overlapping effects in the experimental design. Five sampling sites were selected (Fig. 1). The main characteristics of these locations are

summarized in Table 1. Three woody species were targeted in this study: the wildcherry, the hawthorn, and the bilberry. These species were selected because they are largely dependent on cross-pollination to produce fruit (Gutián and others 1992a; Stern and others 2007), are wide spread in the region, and represent an important feeding resource for many species, some of them particularly important for conservation such as the brown bear (Naves and others 2006; Rodríguez and others 2007) or the capercaillie (Selås 2001; Gregersen and Gregersen 2008).

At each sampling site, a transect was established from the apiary outwards, up to ca. 1400 m, depending on site accessibility and the presence of target species (Table 2). Although honeybees can eventually fly up to seven miles to forage, the economical distance for honey-gathering is sometimes no more than one-quarter of a mile (i.e. approximately 800 m), particularly under adverse weather conditions (Ribbands 1951); therefore it was expected to have absence of honeybees, or at least foraging activity at very low densities, at the end of these transects. In January and early February 2008 all target species were identified and tagged along each of the five transects. For wildcherry and hawthorn, four branches were selected from each individual tree/shrub, two of which were bagged in a 2-mm nylon mesh enclosure to avoid insect pollination, whereas the other two were left uncovered. Each branch represented a sampling. In the case of bilberry, the sampling scheme was slightly different as bilberry twigs are short (just a few

Table 1 Main characteristics of the five study sites in the Cantabrian mountains

Sampling site	Aguino	La Ermita	Navarrega	Pandiella	Peloño
Longitude (°)	-6,267	-6,301	-5,011	-6,151	-5,119
Latitude (°)	43,109	43,312	43,372	43,247	43,149
Altitudinal range (m)	795–875	330–570	250–520	471–593	929–1134
Main vegetation	Open oak forest (<i>Quercus ilex</i> and <i>Q. petraea</i>)	Mixed forest dominated by chestnut (<i>Castanea sativa</i>) interspersed with pastureland and shrubland	Shrubland and pastureland interspersed with fruit trees and chestnuts	Mixed forest dominated by chestnut (<i>Castanea sativa</i>), English oak (<i>Quercus robur</i>) and elder (<i>Sambucus nigra</i>)	Beech forest
Species sampled	Wildcherry, Hawthorn	Wildcherry, Hawthorn, Bilberry	Wildcherry, Hawthorn	Wildcherry, Hawthorn, Bilberry	Wildcherry, Hawthorn, Bilberry
Number of hives	8	4	40	20	7

Table 2 Number of sampling sites and maximum distance from apiary (m) where each species was recorded, number of individual trees/shrubs sampled, and summary of the total, mean and maximum number of flowers and fruits recorded for each species

	Species		
	Wildcherry	Hawthorn	Bilberry
N. of sampling sites	5	5	3
Maximum distance from apiary (m)	1100	1171	1391
N. of individual trees/shrubs sampled ^a	17	20	34
N. of branches sampled			
Control	34	40	17
Nylon mesh	34	40	17
N. of branches sampled with n. flowers $\geq 10^b$			
Control	32	16	5
Nylon mesh	34	10	7
Total number of flowers			
Control	5160	1437	104
Nylon mesh	4129	1151	129
Mean number of flowers			
Control	161.2	89.8	20.8
Nylon mesh	121.4	115.1	18.4
Maximum number of flowers			
Control	939	333	36
Nylon mesh	486	522	37
Total number of fruits			
Control	885	218	32
Nylon mesh	212	53	23
Mean number of fruits			
Control	27.6	13.6	6.4
Nylon mesh	6.2	5.3	3.2
Maximum number of fruits			
Control	121	109	26
Nylon mesh	60	30	13

^a In the case of bilberry, each sample consisted of five branches taken from the same site and pooled together for data analysis

^b In the case of bilberry, the minimum number of flowers required for analysis was five

centimeters) and produce few flowers compared to the other two species. To obtain representative sample units, ten twigs were selected at each individual bush: five were bagged in a 2-mm nylon mesh enclosure, and the other five were left uncovered. Each group of five twigs in each bilberry bush represented a sampling unit.

From late February to October 2008 sampling sites were visited every two to three weeks. Flowers were first counted and fruit production was measured thereafter. The response variable was *fruit set*, i.e. the proportion of flowers that produced fruits, a measure of pollination success. To obtain a robust measure of *fruit set*, only

branches with more than ten flowers were used for analyses, except for the bilberry, where the minimum number of flowers required for analysis was five. A summary of the sampling effort conducted in this study is shown in Table 2.

Statistical Analyses

We identified variables that significantly affected the probability of *fruit set* for each species using generalized linear mixed-effects models (McCullagh and Nelder 1989) with a binomial error distribution and a logit link function. Mixed-effects models are appropriate for representing clustered and therefore potentially autocorrelated data (Pinheiro and Bates 2000), as it is the case of samples aggregated within individual plants and locations. In this particular case, random variability in the response variable may stem from: (1) differences in fruit set performance caused by the plant identity; and (2) differences in topography, surrounding vegetation and number of hives at each sampling site. Because each plant was only located at one sampling site, plant identity was nested within location.

The proposed model was stated as follows:

$$\text{fruit set} = \text{distance} + \text{exclosure} + \text{distance} * \text{exclosure} \\ + \text{plant} : \text{location}$$

where: *fruit set* = proportion of flowers that produced fruits; *distance* = distance to apiary (m); *exclosure* = a two level factor specifying whether the branch/twig had been bagged in a nylon mesh exclosure (*control*) or not (*treatment*); *plant:location* = a random term specifying the effect of individual plants, nested within each one of the five studied locations.

We explored the effects of random effects on the model intercept (i.e., how individual plants and/or sites can affect fruit set performance) but also on the treatment effects (i.e., how individual plants and/or sites can influence the observed differences between fruit set performance in bagged and non-bagged samples). Following Zuur and others (2007) we compared models with different random error structure using the restricted maximum likelihood (REML) estimation procedure. As for the fixed effects, we were specifically interested in testing the significance of the effects of the interaction between *distance* to the apiary and the nylon mesh *exclosure* on fruit set. Our hypothesis was that, if honeybees have an effect on *fruit set* for a particular species, there should be a negative relationship between *fruit set* and *distance* to the apiary for non-bagged samples (*treatment*), and a null effect on samples bagged in a nylon mesh exclosure (*control*). These effects are accounted for by the interaction between both variables (*distance* to apiary and *exclosure*). To help interpret the effects of such

interaction, we represented the estimated values of *fruit set* for both exclosure (*control*) and non-bagged (*treatment*) samples as a function of *distance* to the apiary according to the resulting models. All analyses were conducted with the R package ‘lme4’ (Bates and others 2008).

Results

Total, mean and maximum number of flowers and fruits recorded for each species can be found in Table 2. Our results showed that the effect of distance in itself was not significant in all three models (Table 3). The *exclosure* (*control*) produced a significantly lower fruit set in all three species as compared to non-bagged (*treatment*) samples (Table 3). The interaction between *distance* to apiary and *exclosure* was significant only for hawthorn and bilberry (Table 3). Non-bagged samples of wildcherry produced only a slightly higher amount of fruits than exclosure samples, regardless of *distance* to the apiary (Fig. 2a). Models predicted a decrease in *fruit set* of hawthorn from about 10% to 0% over a distance of approximately 750 m from the apiary (Fig. 2b), whereas this decrease spanned from 100% to 0% in the case of bilberry over the same distance range (Fig. 2c).

Discussion

Impact of Honeybees on Fruit Set and Wildlife Conservation

The fruit yields observed in this study demonstrate that honeybee activity significantly increases pollination and fruit set in two out of the three native plant species investigated. Although the results for bilberry are based on a small number of samples, it is important to note that each sample is a compound measure of five twigs and does therefore represent a robust estimate of *fruit set*. The low levels of *fruit set* found for hawthorn contrast with those found for bilberry. Guitián and others (1992b), however, reported similar levels of fruit set (<30%) for hawthorn, *Prunus mahaleb* L. and *P. spinosa* L., even in the presence of pollinators. They argued that fruit production in these species is limited by intrinsic factors (e.g., adaptive life history associated with reproductive effort) rather than simply the result of insufficient pollination (see also Ashman and others 2004; Brown and McNeil 2006; Knight and others 2006). Our results for wildcherry indicate that wild pollinators, at least in our study area, can successfully replace honeybees to efficiently pollinate this tree. Fruit set in this case, as for hawthorn and other Rosaceae (Guitián and others 1992b), is very low, possibly due to intrinsic

Table 3 Results of the generalized linear mixed-effects models for the three studied species

Wildcherry (<i>Prunus avium</i>)				
Random effects	Variance	Std. Dev.		
Tree in sampling site (intercept)	4.410	2.100		
Tree in sampling site (treatment)	2.970	1.723		
Fixed effects	Estimate	Std. error	z value	Pr(> z)
Intercept	-4.638	1.582	-2.932	0.003
Distance	0.002	0.003	0.753	0.451
Treatment (non-bagged)	2.432	0.232	10.500	<2e-16
Treatment * Distance	-0.003	0.001	-3.493	4.77e-04
Hawthorn (<i>Crataegus monogyna</i>)				
Random effects	Variance	Std. Dev.		
Tree in sampling site (intercept)	6.017	2.435		
Fixed effects	Estimate	Std. error	z value	Pr(> z)
Intercept	-4.255	0.971	-4.382	0.000
Distance	0.000	0.001	-0.006	0.996
Treatment (non-bagged)	2.319	0.235	9.852	0.000
Treatment * Distance	-0.003	0.001	-3.792	0.000
Bilberry (<i>Vaccinium myrtillus</i>)				
Random effects	Variance	Std. Dev.		
Shrub in sampling site (intercept)	3.433	1.853		
Fixed effects	Estimate	Std. error	z value	Pr(> z)
Intercept	-2.384	2.032	-1.173	0.241
Distance	2.40e-04	0.003	0.081	0.935
Treatment (non-bagged)	7.309	1.538	4.751	2.03e-06
Treatment * Distance	-0.010	0.002	-4.533	5.82e-06

The estimated variance and standard deviation are shown for the random effects. The estimated coefficient and standard error, z-value and p-value are shown for the fixed terms, including the interaction between the two main explanatory variables. Significant values at $p < 0.05$ are shown in bold

factors that limit fruit production. Although we have not tested this hypothesis specifically, our results seem to indicate that both intrinsic factors and pollination are important in determining fruit set. Other species that strongly depend on insect pollination, such as *P. spinosa* or *P. mahaleb* (Gutián and others 1992a), have been reported as visited more frequently by honeybees than by any other pollinator.

From a conservation perspective, different studies have investigated the effect of honeybees on endemic, rare or threatened plant populations, reporting either positive (Gross 2001; Chamberlain and Schlising 2008), negative (Gross and Mackay 1998), or neutral effects (Dupont and others 2004) when compared to the performance of wild pollinators. The role of honeybees for pollination of native

plants can however have wider effects for other trophic levels. Many species feed on fruits produced by shrubs and trees. Such fruits may constitute an important feeding resource during certain periods of the year. For example, berries, fleshy fruits, and hard mast constitute the bulk of the brown bear diet during the hyperphagic season, i.e. the period that follows the mating season when the bear's food intake increases markedly (June–July), allowing them to gain weight until they enter a den for hibernation in November–December (Naves and others 2006; Rodríguez and others 2007). Bilberries have been reported to constitute 11.3% of the volume of the bear's diet during this season, followed by *Prunus* fruits (*P. avium*, *P. domestica* L., *P. persica* L. (Batsch.), *P. spinosa*) (6.8%), and hawthorn berries (0.8%) (Naves and others 2006). Although

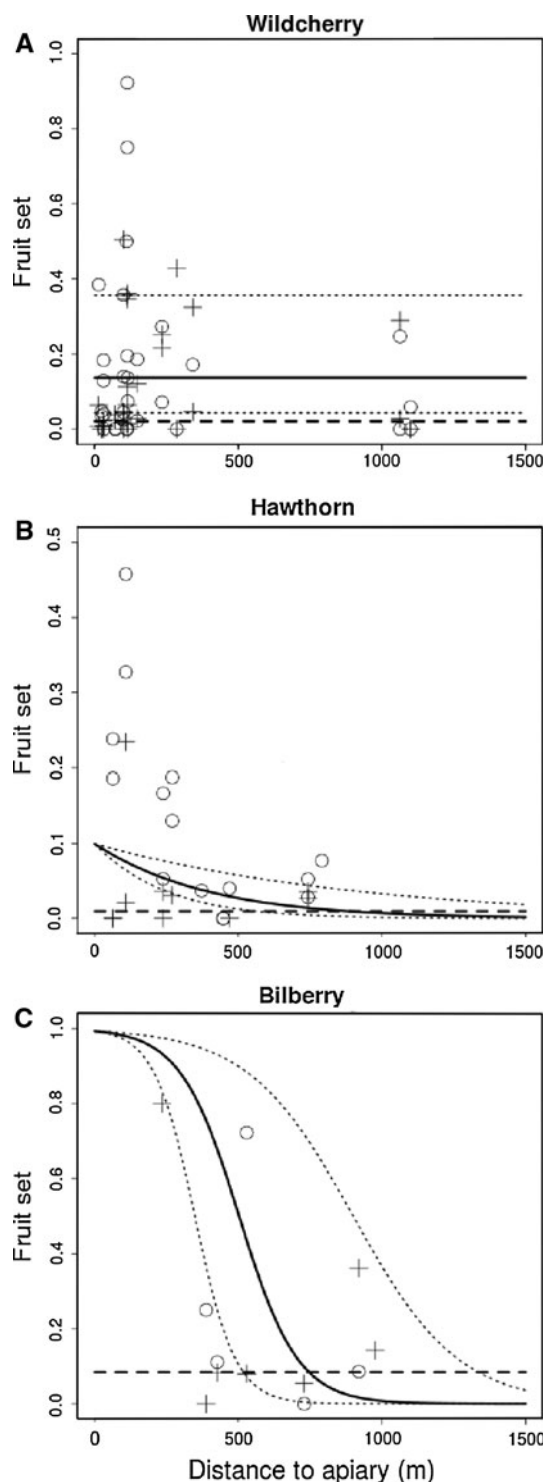


Fig. 2 Estimated effects of distance to apiary on fruit set for enclosure (dashed lines) and non-bagged samples (solid lines) for the wildcherry (a), the hawthorn (b) and the bilberry (c). Fruit set was calculated as the proportion of flowers that produced fruits, as a measure of pollination success. Dotted lines represent 95% confidence intervals for the models' estimates in the case of non-bagged samples. Observed values are also represented for enclosure (crosses) and non-bagged (circles) samples

there are no studies demonstrating that populations of bear are limited by food, two factors are likely to turn out food shortage a serious problem: (1) a recovery of bear populations in the Cantabrian Mountains (Palomero 2007) which may be followed by increasingly intra-specific competition for resources; and (2) the problem of the lack of carrion for bears. Traditionally, dead livestock was left abandoned or dumped in the mountains, but a recent EU law now prohibits this practice because of fears of mad cow disease.

The Honeybees Versus Wild Bees Debate

In recent years, an intense debate has developed around the respective contribution of wild and managed pollination service components (Allsopp and others 2008), as well as on the impact of honeybees on native flora and fauna. Results of some studies suggest that foraging patterns and abundance of wild pollinators are altered in the presence of honeybees (Roubik 1978; Schaffer and others 1983; Paton 1993; Vaughton 1996; Gross and Mackay 1998; Gross 2001; Hansen and others 2002; Forup and Memmott 2005; Thomson 2006). Although stressed as important by most researchers, the potential detrimental effects of introduced honeybees on food storage or on reproduction of native bee species have been difficult to investigate (Butz Huryn 1997; Steffan-Dewenter and Tschardt 2000), and no studies to date have documented local extinction of native bees caused by *Apis mellifera* (Forup and Memmott 2005; Moritz and others 2005). The impact of honeybees on the pollination of native flora includes effects on pollen dispersal and thus patterns of seed set and genetic structure of plant populations. Honeybees are often found to be less efficient pollinators compared to native flower-visiting animals (Schaffer and others 1983; Taylor and Whelan 1988; Westerkamp 1991; Paton 1993; Vaughton 1996; Gross and Mackay 1998; Hansen and others 2002). However, other studies have found that *A. mellifera* does not adversely affect plant reproductive success, perhaps due to the numerical abundance of honeybees compared to wild bees (Vaughton 1992; Gross 2001; Dupont and others 2004).

In most environments, both wild pollinators and honeybees will exploit flowers of both crops and native flora (Klein and others 2007). Honeybees are undoubtedly important pollinators due to their high demand for pollen and nectar, their hairy body, which collects and disperses the pollen, and the high number of bees that can live in a single hive (30–50 thousand bees, Stern and others 2007). For example, Heinrich (1979) calculated that a single, large apiary in the USA would collect the equivalent amount of nectar and pollen to support 38,400 bumblebee

reproductives, or 102 colonies in one year (Forup and Memmott 2005). In addition, because *A. mellifera* colonies persist longer than most native bee species, it may be a more reliable pollinator throughout a season than species that have shorter activity periods (Chamberlain and Schlising 2008). Other bee species, on the contrary, have proved to be more efficient pollinators than honeybees for certain plant species due to specific co-evolutionary traits (Westerkamp 1991). Bumblebees, for example, have been reported to pollinate bilberry flowers more effectively than honeybees, both in terms of fruit set and quality (Nuortila and others 2002; Raspe and others 2004; Ratti and others 2008). Pollination of certain species might prove most efficient when both honeybees and wild pollinators are present. For example, strawberry flowers visited by both wild bees and honeybees are more likely to achieve complete development in contrast with flowers that are visited by only honeybees or only wild bees, that tend to have misshapen fruits (Chagnon and others 1993; Greenleaf and Kremen 2006). These effects have rarely been investigated, but may prove to be widespread (Klein and others 2007). Thus, in the view of these studies and our own results, we advocate for the preservation of traditional apicultural practices in rural areas where low density of hives are unlikely to cause any harm to wild pollinators, while augmenting pollination services and increasing fruit set for some native plant species that are key feeding resource for wildlife species of conservation concern.

Conservation in Practice

Given the current situation of land abandonment (MacDonald and others 2000) and the decline of honeybees in rural agroecosystems of northern Spain, a suitable option to increase fruit set as a measure to provide more feeding resources for different animal species would consist in promoting the recovery of traditional apicultural practices at low densities. This initiative may also contribute to develop a secondary economic activity, particularly in rural areas, where it provides a supplementary income, which helps fix the rural population, therefore contributing to the amelioration of the environmental impacts resulting from land abandonment (MacDonald and others 2000). In the study region, a non governmental organization (*Fondo para la Protección de los Animales Salvajes*) has been leading a conservation initiative to promote pollination of native plants since 1999 and, to date, almost 540 hives have been allocated in 69 sites in mountain agroecosystems. These hives are left in charge of local farmers that can exploit them for their own benefit. Further investigation is

required to determine the specific honeybee densities that are desirable to promote fruit set of native plants without interfering much in the dynamics of other native pollinators. This might help establish general guidelines for best practices of honeybee management in order to implement a broad scale honeybee recovery program.

Although this study has shed some light on the importance of honeybees as pollinators of some native plant species, further studies such as long-term research that incorporates inter-annual variability in fruit production, evaluation of the relative importance of fruit size/mass vs. fruit set for plant fitness, pollen limitation in the absence of honeybees, quantification of cross-pollination vs. self-pollination, and assessment of factors affecting fruit set others than pollination are needed. More studies are also needed to investigate the role and functions of wild pollinators so actions for conservation and enhancement of their populations could be also implemented as a complementary alternative to the ones proposed in this study.

Conclusions

This study assessed the importance of honeybees for the pollination of three native plant species whose fruits are important feeding resources for many animal species, including the endangered brown bear and the capercaillie in northern Spain. Whereas no effects of distance to the apiary were found for wildcherry, significant effects were found for hawthorn and bilberry. This suggests that the use of honeybees as pollinating agents under traditional farming practices may be an effective instrument to increase fruit production of, at least, some native plants, and therefore increase availability of feeding resources for wildlife species of conservation value. In addition to the pollination service they provide, honeybees constitute a secondary economic activity, particularly in rural areas, where they provide a supplementary income. Therefore, mechanisms that promote and stimulate traditional apiculture in mountain areas are likely to generate economic, environmental and conservation benefits.

Acknowledgments This project was commissioned by *Fondo para la Protección de los Animales Salvajes* (FAPAS) through a two year grant from *Fundación Biodiversidad (Recuperación de la abeja (Apis mellifera) en estado silvestre y reforzamiento de la polinización de ecosistemas de montaña en la Cordillera Cantábrica)*. LC was supported by the Andalusian Regional Government project GESBOME (P06-RNM-1890). We are indebted to R. Hartasánchez for his stimulating ideas and M. Méndez for fruitful discussions on conceptual and methodological issues related to this research. Many thanks also to L. Gálvez, J.M. Rey Benayas, J. Herrero (Brown Bear Foundation), and R. Zamora for their useful comments on a former version of this manuscript.

References

- Allsopp MH, de Lange WJ, Veldtman R (2008) Valuing insect pollination services with cost of replacement. *PLOS One* 3(9):1–8
- Ashman T-L, Knight TM, Steets JA, Amarasekare P, Burd M, Campbell DR, Dudash MR, Johnston MO, Mazer SJ, Mitchell RJ, Morgan MT, Wilson WG (2004) Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. *Ecology* 85:2408–2421
- Bates D, Maechler M, Dai B (2008) lme4: Linear-mixed-effects models using Eigen and Eigen. R package version 0.999375-20. <http://lme4.r-forge.r-project.org/>
- Brown AO, McNeil JN (2006) Fruit production in cranberry (*Ericaceae: Vaccinium macrocarpon*): a bet-hedging strategy to optimize reproductive effort. *American Journal of Botany* 93(6):910–916
- Bulboa Cortés MC, Martínez Avilés M (2007) Análisis de riesgo en la entrada y difusión de los agentes que pueden afectar a las abejas melíferas en España. *Revista Complutense de Ciencias Veterinarias* 1(2):56–62
- Butz Huryn VM (1997) Ecological impacts of introduce honey bees. *The Quarterly Review of Biology* 72:275–297
- Chagnon M, Gingras J, De Oliveira D (1993) Complementary aspects of strawberry pollination by honey and indigenous bees (Hymenoptera). *Journal of Economic Entomology* 86:416–420
- Chamberlain SA, Schlising RA (2008) Role of honey bees (Hymenoptera: Apidae) in the pollination biology of a California native plant, *Triteleia laxa* (Asparagales: Themidaceae). *Environmental Entomology* 37(3):808–816
- Chen Y, Pettis JS, Evans JD, Kramer M, Feldlaufer MF (2004) Transmission of Kashmir bee virus by the ectoparasitic mite *Varroa destructor*. *Apidologie* 35:441–448
- Dedej S, Delaplane KS (2003) Honey bee (Hymenoptera: Apidae) pollination of rabbiteye blueberry *Vaccinium ashei* var. ‘Climax’ is pollinator density-dependent. *Horticultural Entomology* 96(4):1215–1220
- Degrandi-Hoffman G, Chambers M (2006) Effects of honey bee (Hymenoptera: Apidae) foraging on seed set in self-fertile sunflowers (*Helianthus annuus* L.). *Environmental Entomology* 35(4):1103–1108
- Delaplane KS, Mayer DF (2000) Crop pollination by bees. CABI Publishing, New York
- Downey DL, Winston ML (2001) Honey bee colony mortality and productivity with single and dual infestation of parasitic mite species. *Apidologie* 32:567–575
- Dupont YL, Hansen DM, Valido A, Olesen JM (2004) Impact of introduced honey bees on native pollination interactions of the endemic *Echium wildpretii* (Boraginaceae) on Tenerife, Canary Islands. *Biological Conservation* 118:301–311
- Ellis JD, Evans JD, Pettis J (2010) Colony losses, managed colony population decline, and colony collapse disorder in the United States. *Journal of Apicultural Research* 49(1):134–136
- Evans JD, Pettis JS, Hood WM, Shimanuki H (2003) Tracking an invasive honey bee pest: mitochondrial DNA variation in North American small-hive beetles. *Apidologie* 34:103–109
- Forup ML, Memmott J (2005) The relationship between the abundances of bumblebees and honeybees in a native habitat. *Ecological Entomology* 30:47–57
- Gogoi B, Rahman A, Rahman S, Deka MK (2007) Foraging behaviour and effect of *Apis cerana* pollination on fruit set and yield of Assam lemon (*Citrus limon*). *Indian Journal of Agricultural Sciences* 77(2):120–122
- Gómez-Sal A (1994) The rural landscapes of northern Spain. *Landscape Issues* 11(1):5–12
- Goodman R, Hepworth G, Kaczynski P, McKee BA, Clarke SJ, Bluett C (2001) Honeybee pollination of buckwheat (*Fagopyrum esculentum* Moench) cv. Manor. *Australian Journal of Experimental Agriculture* 41:1217–1221
- Greenleaf SS, Kremen C (2006) Wild bees enhance honey bees’ pollination of hybrid sunflower. *Proceedings of the National Academy of Sciences* 103:13890–13895
- Gregersen H, Gregersen F (2008) Old bilberry forest increases likelihood of Capercaillie *Tetrao urogallus* lek occupancy in Southern Norway. *Ornis Norvegica* 31:105–115
- Gross CL (2001) The effect of introduced honeybees on native bee visitation and fruit-set in *Dillwynia juniperina* (Fabaceae) in a fragmented ecosystem. *Biological Conservation* 102:89–95
- Gross CL, Mackay D (1998) Honeybees reduce fitness in the pioneer shrub *Melastoma affine* (Melastomataceae). *Biological Conservation* 86:169–178
- Guitián J, Guitián P, Sánchez JM (1992a) Reproductive biology of two *Prunus* species (Rosaceae) in the Northwest Iberian Peninsula. *Plant Systematics and Evolution* 185:153–165
- Guitián J, Sánchez JM, Guitián P (1992b) Niveles de fructificación en *Crataegus monogyna* Jacq., *Prunus mahaleb* L. y *Prunus spinosa* L. (Rosaceae). *Anales Jardín Botánico de Madrid* 50(2):239–244
- Hansen DM, Olesen JM, Jones CG (2002) Trees, birds and bees in Mauritius: exploitative competition between introduced honey bees and endemic nectarivorous birds. *Journal of Biogeography* 29:721–734
- Heinrich B (1979) Bumblebee economics. Harvard University Press, Cambridge
- Higes M, Martin R, Meana A (2006) *Nosema ceranae*, a new microsporidian parasite in honeybees in Europe. *Journal of Invasive Pathology* 92:93–95
- Ingram M, Nabhan GC, Buchmann SL (1996) Impending pollination crisis threatens biodiversity and agriculture. *Tropinet* 7:1
- Kearns CA, Inouye DW, Waser N (1998) Endangered mutualisms: the conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics* 29:83–112
- Kevan PG, Phillips TP (2001) The economic impacts of pollinator declines: an approach to assessing the consequences. *Conservation Ecology* 5(1):8
- Klein A-M, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society Series B-Biological Sciences* 274:303–313
- Knight TM, Steets JA, Sahman T-L (2006) A quantitative synthesis of pollen supplementation experiments highlights the contribution of resource allocation to estimates of pollen limitation. *American Journal of Botany* 93:271–277
- MacDonald D, Crabtree JR, Wiesinger G, Dax T, Stamou N, Fleury P, Gutierrez Lazpita J, Gibon A (2000) Agricultural abandonment in mountain areas of Europe: environmental consequences and policy response. *Journal of Environmental Management* 59(1):47–69
- Manning R, Boland J (2000) A preliminary investigation into honey bee (*Apis mellifera*) pollination of canola (*Brassica napus* cv. Karoo) in Western Australia. *Australian Journal of Experimental Agriculture* 40:439–442
- Manning R, Wallis IR (2005) Seed yields in canola (*Brassica napus* cv. Karoo) depend on the distance of plants from honeybee apiaries. *Australian Journal of Experimental Agriculture* 45:1307–1313
- Matheson A, Buchmann SL, O’Toole C, Westrich P, Williams IH (1996) The conservation of bees. Academic Press, London, UK
- McCullagh P, Nelder JA (1989) Generalized linear models, 2nd edn. Chapman and Hall/CRC, New York

- Moritz RFA, Härtel S, Neumann P (2005) Global invasions of the western honeybee (*Apis mellifera*) and the consequences for biodiversity. *Ecoscience* 12:289–301
- Naves J, Fernández-Gil A, Rodríguez C, Delibes M (2006) Brown bear food habits at the border of its range: a long-term study. *Journal of Mammalogy* 87(5):899–908
- Nuortila C, Tuomi J, Laine K (2002) Inter-parent distance affects reproductive success in two clonal dwarf shrubs, *Vaccinium myrtillus* and *Vaccinium vitis-idaea* (Ericaceae). *Canadian Journal of Botany* 80:875–884
- Oz M, Karasu A, Cakmak I, Goksoy AT, Ozmen N (2008) Effect of honeybees pollination on seed setting, yield and quality characteristics of rapeseed (*Brassica napus oleifera*). *Indian Journal of Agricultural Sciences* 78(8):680–683
- Palomero G (2007) *Ursus arctos* Linnaeus, 1758. In: Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y Libro Rojo de los Mamíferos Terrestres de España. Dirección General para la Biodiversidad – SECEM – SECEMU, Madrid
- Paton DC (1993) Honeybees in the Australian environment. *BioScience* 43:95–103
- Pinheiro JC, Bates DM (2000) Mixed-Effects Models in S and S-PLUS. Statistics and computing. Springer, New York
- Potts SG, Roberts SPM, Dean R, Marris G, Brown MA, Jones R, Neumann P, Settele J (2010) Declines of managed honey bees and beekeepers in Europe. *Journal of Apicultural Research* 49(1):15–22
- Racys J, Montviliene R (2005) Effects of bees-pollinators in Buckwheat (*Fagopyrum esculentum* Moench) crops. *Journal of Apicultural Science* 49(1):47–51
- Raspe O, Guillaume P, Jacquemart AL (2004) Inbreeding depression and biased paternity after mixed-pollination in *Vaccinium myrtillus* L. (Ericaceae). *International Journal of Plant Sciences* 165:765–771
- Ratti CM, Higo HA, Griswold TL, Winston ML (2008) Bumble bees influence berry size in commercial *Vaccinium* sp. cultivation in British Columbia. *Canadian Entomologist* 140:348–363
- Rhodes J (2002) Cotton pollination by honey bees. *Australian Journal of Experimental Agriculture* 42:513–518
- Ribbands CR (1951) The flight range of the honey-bee. *Journal of Animal Ecology* 20(2):220–226
- Rodríguez C, Naves J, Fernández-Gil A, Obeso JR, Delibes M (2007) Long-term trends in food habits of a relict brown bear population in northern Spain: the influence of climate and local factors. *Environmental Conservation* 34(1):36–44
- Roubik DW (1978) Competitive interactions between neotropical pollinators and Africanized honey bees. *Science* 201:103–1032
- Sánchez LA, Picado A, Sommeijer MJ, Slaa EJ (2002) Floral biology, pollination ecology and seed production of the ornamental plant *Salvia splendens* Sello. *Journal of Horticultural Science and Biotechnology* 77(4):498–501
- Schaffer WM, Zeh DW, Buchmann SL, Kleinhans S, Schaffer MV, Antrim J (1983) Competition for nectar between introduced honeybees (*Apis mellifera*) and native North American bees and ants. *Ecology* 64:546–577
- Selås V (2001) Autumn population size of capercaillie *Tetrao urogallus* in relation to bilberry *Vaccinium myrtillus* production and weather: an analysis of Norwegian game reports. *Wildlife Biology* 7:17–25
- Southwick EE, Southwick L Jr (1992) Estimating the economic value of honey bees (Hymenoptera: Apidae) as agricultural pollinators in the United States. *Journal of Economic Entomology* 85:621–633
- Steffan-Dewenter I, Tschamtk T (2000) Resource overlap and possible competition between honey bees and wild bees in central Europe. *Oecologia* 122:288–296
- Stern RA, Sapir G, Shafir S, Dag A, Goldway M (2007) The appropriate management of honey bee colonies for pollination of *Rosaceae* fruit trees in warm climates. *Middle Eastern and Russian Journal of Plant Science and Biotechnology* 1(1):13–19
- Storch I, Bañuelos MJ, Fernández-Gil A, Obeso JR, Quevedo M, Rodríguez-Muñoz R (2006) Subspecies Cantabrian capercaillie *Tetrao urogallus cantabricus* endangered according to IUCN criteria. *Journal of Ornithology* 147:653–655
- Taylor G, Whelan RJ (1988) Can honeybees pollinate *Grevillea*? *Australian Zoologist* 24:193–196
- Thomson DM (2006) Detecting the effects of introduced species: a case study of competition between *Apis* and *Bombus*. *Oikos* 114:407–418
- Vaughton G (1992) Effectiveness of nectarivorous birds and honeybees as pollinators of *Banksia spinulosa* (Proteaceae). *Australian Journal of Ecology* 17:43–50
- Vaughton G (1996) Pollination disruption by European honeybees in the Australian bird-pollinated shrub *Grevillea barklyana* (Proteaceae). *Plant Systematics and Evolution* 200:89–100
- Watanabe ME (1994) Pollination worries rise as honey bees decline. *Science* 265:1170
- Westerkamp C (1991) Honeybees are poor pollinators—why? *Plant Systematics and Evolution* 177:71–75
- Williams IH, Corbet SA, Osborne JL (1991) Beekeeping, wild bees and pollination in the European community. *Bee World* 72:170–180
- Zuur AF, Ieno EN, Smith GM (2007) Analysing ecological data. Springer, New York, USA