

HONEYBEE (*APIS MELLIFERA*) MEDIATED INCREASED REPRODUCTIVE SUCCESS OF A RARE DECEPTIVE ORCHID

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Abstract. Honeybees are the most numerous and significant among insect pollinators, but despite their significance their potential role in increasing the reproductive success of threatened European orchids remains largely unexplored. In this study we aim to evaluate the effect of apiary proximity on the fructification rate of the rare and endangered Adriatic Lizard Orchid (*Himantoglossum adriaticum* H. Baumann). To do so, first we quantified the reproductive success (fruit set) of the Adriatic Lizard Orchids in a Hungarian population in close proximity to a honeybee apiary at Nagytevel. Then we compared the reproductive success in this population to the reproductive success in 3 other Hungarian, 4 Croatian populations (observed during the same year, 2013) and further 4 populations from Hungary (studied in previous years, 1992–2011) with no apiaries in the close proximity of these. The realised 61.7 % fruit set at Nagytevel is the highest reproductive success ever recorded for this species. The importance of apiaries is further emphasised by the fact that the reproductive success of Lizard Orchid individuals decreased significantly with increasing distance from the apiary. Our results provide empirical support for the conservation importance of apiculture and suggest promising results for practical application of apiaries in the conservation of deceptively pollinated orchids characterised by lower fruit set (e.g. *Orchis*, *Anacamptis*, *Himantoglossum*).

Keywords: *apiculture, fruit set, Himantoglossum adriaticum, pollination crisis, Orchidaceae*

Introduction

The family *Orchidaceae*, with its more than 25,000 species, is one of the largest in the plant kingdom (Dressler, 1993). Despite their world-wide dispersion and extreme plasticity, the majority of these species are of key conservation importance (Jacquemyn et al., 2005; Kull and Hutchings, 2006; Swarts and Dixon; 2009). Causes of their decline are complex, but – independently of the conservation status – the long-term persistence of plant populations in every case partly depends on seed production.

The reproductive success of entomophilous orchids depends on the effectiveness of pollination processes, namely; pollinator attraction, pollen sack removal and its deposition on conspecific flower. Such interactions have immediate consequences for

endangered *Spiranthes* species, as increases in both conspecific and heterospecific coflowering density may ameliorate the negative effects of rarity on pollination, hence overall reproductive success (Duffy and Stout, 2011). Lack of suitable insects to pollinate the flowers of *Orchis militaris* has been characteristic of British populations since the beginning of 19th century according to herbaria data (Farrell, 1985). Similar low fruit set were detected at the beginning of 20th century in Germany (Sprengel, reported by Godfrey 1933).

The flowers of deceptive (i.e. non-rewarding) orchids usually experience very low pollinator visitation rates that will result in low levels of fruit set compared to rewarding orchids (Dafni and Ivri, 1979; Gill, 1989; Neiland and Wilcock, 1999; Harder and Johnson, 2008). Deception is not rare among the orchids, it is estimated that as much as one-third of orchid species use various forms of floral deception to attract pollinators (Dafni, 1984; Ackerman, 1986; Jersáková et al., 2006).

In temperate climate regions the most important pollinators are insects, among which bees predominate. It was the finding of the last decades that bees in parallel with insect-pollinated plants are declining on both western European (Biesmeijer et al., 2006) and global scales (Allen-Wardell et al., 1998; Kearns et al., 1998; Potts et al., 2010). The major threat to bee diversity is habitat loss, but competitive invasive species, newly emerging diseases, extensive use of pesticides, and climate change also have the potential to negatively impact bee population sizes (Brown and Paxton, 2009; Brittain and Potts, 2011). Bees require a large number of flowers to gather enough nectar and pollen to support the hive, and also need a large variety of flowering plants with different flowering times to provide them continuous food supplies throughout the growing season (Kearns and Inoyue, 1997). However, due to the relatively recent change in land-use practices, the nectar sources for bees, characteristic to fragmented landscapes have greatly diminished in recent years (Feon et al., 2013).

Despite the dominant individual number of honeybee in the bee assemblages and their importance in pollination, the potential role in the reproductive success of European orchids remains largely unclear.

The aim of the present study was to evaluate the role of apiculture in increasing the reproductive success of the rare and endangered Adriatic Lizard Orchid (*Himantoglossum adriaticum* Baumann). Red Data Books of most countries where it occurs (Conti et al., 1997; Király 2007; Maglocky and Feráková, 1993; Grulich, 2012). The conservation status of the species is Critically Endangered in the Czech Republic and in Slovakia, Endangered in Austria and in Hungary, Vulnerable in Slovenia and Near Threatened in Croatia (Dostalova et al., 2011). Additionally *H. adriaticum* is suffering ongoing population declines and is listed in the Annex II of Council Directive 92/43/EEC (the 'Habitats Directive').

The reproductive success of *Himantoglossum adriaticum* is generally low. Previously published fruit set data varied between 4.5 and 44 % in Austria (Vöth, 1990), and between 5.4% and 23.3% in Hungary (Bódis and Molnár, 2009).

We measured reproductive success (fruit set) in a population of Adriatic Lizard Orchid in close proximity to a honeybee colony and compared it with other populations observed during the same year without bees and four populations studied in previous years.

An apiary, composed of 174 hives hosting *Apis mellifera* colonies in 4 containers was located on the study site at Nagytevel (Hungary) between 25th May and 05th July 2013 (coinciding with the flowering time of *Himantoglossum* orchids). The distance of

the hives from flowering *Himantoglossum* plants varied between 196–1455 meters. All studied *H. adriaticum* flowering specimens were situated within the effective foraging radius (1.5–3 km, Frisch, 1965; Bagella et al., 2013) of honeybees in Europe. To the best of our knowledge, no apiaries were present in the vicinity of this population in other years, nor in the rest of populations studied here.

We specifically stated the following study questions: (i) Is there significant effect of the apiary on the reproductive success of *H. adriaticum* population, living within the foraging distance of honeybee? (ii) Is there correlation between the individual reproductive success (fruit set) and the distances from the apiary?

Materials and methods

Study species

Himantoglossum adriaticum H. Baumann has a central submediterranean distribution, currently known to occur in Croatia, Slovenia, northern and central Italy, eastern Austria, western Slovakia and Hungary (Pecoraro et al., 2013, Rybka et al., 2005).

The characteristic habitat of the species is full sun to mid-shade and dry calcareous substrates. It prefers poor grassland, banks, thickets, woodland edges and open woodlands, up to 1600 meters of altitude above sea level (Delforge, 2006), relatively often occurring in secondary habitats, e.g. abandoned vine-yards, extensively used orchards and mown grassy verges on the sides of public roads (Molnár, 2011). The Adriatic Lizard Orchid is a terrestrial, tuberous photoautotrophic orchid with overwintering rosette, which consists of 2–7 large, lanceolate, pale green basal leaves. The generative shoots are 30–80 cm tall, the inflorescence is elongated and lax, composed of 15–40 brownish red, typically malodorous flowers. The lip is deeply 3-lobed, the median lobe is long, ribbon-like, incised (Delforge, 2006; Molnár, 2011). The flowers have been observed to be pollinated by the following bee species: *Andrena haemorrhua*, *A. carbonaria*, *A. nigroaenea*, *A. potentillae*, *Apis mellifera* (Claessens and Kleynen, 2011), *Colletes similis* (Vöth, 1990; Sulyok et al., 1998), *Bombus* spp. (Teschner, 1980), *Osmia caerulea*, *Lasioglossum (Evyllaesus) morio*, *Lasioglossum (Evyllaesus) lucidulum*, *Megachile melanopyga* (Bódis, 2010).

Measuring reproductive success

Eight populations of *Himantoglossum adriaticum* were studied in Hungary and Croatia in 2013 (Table 1).

Table 1. Adriatic Lizard Orchid populations studied in 2013. n: total number of undamaged fruiting shoots observed; Date of observation: flowering and fruiting sampling.

No.	Country	Locality	n	Date of observation	Geocoordinates
1	Hungary	Nagytevel	39	20 th June; 31 st July	N 47.264°, E 17.598°
2	Hungary	Kőszeg	36	19 th June.; 13 rd July	N 47.375°, E 16.526°
3	Hungary	Keszthely	33	15 th June; 14 th July.	N 46.794°, E 17.277°
4	Hungary	Sümeg	47	17 th June; 13 rd July	N 46.957°, E 17.351°
5	Croatia	Učka	88	2 nd –3 rd June; 8 th –9 th July	N 45.317°, E 14.175°
6	Croatia	Paz	7	4 th June; 9 th July	N 45.277°, E 14.104°
7	Croatia	Letaj I.	14	4 th June; 9 th July	N 45.255°, E 14.121°
8	Croatia	Letaj II.	12	4 th June; 9 th July	N 45.255°, E 14.132°

All generative shoots were individually marked with labelled nail. The number of flowers on each specimen was recorded during the first visits on each site (between 2th and 20th June), while the number of developed fruits was counted 3–5 weeks later (between 8th and 31st July). Shoots which were damaged during the flowering period were excluded from the analyses. Reproductive success was defined as fructification rate: total number of fruits in the population divided by the total number of flowers in the given population on a given specimen; in other terms fruit set. The reproductive success of populations were compared to data on the fructification rate of the same species collected in earlier years using the same methodology (Table 2). The reproductive success means in every case population level.

Table 2. Adriatic Lizard Orchid populations studied between 1992–2011. *n*: total number of undamaged fruiting shoots observed in a given population.

No.	Country	Locality	Study period	n
1	Hungary	Nagytevel	2010, 2011	11, 41
2	Hungary	Kőszeg	2010, 2011	33, 18
3	Hungary	Keszthely	1992–2011	17–73
4	Hungary	Sümeg	2002, 2003, 2008–2011	76, 19, 25–49

Data analyses

To compare the reproductive success of different populations we employed a generalized linear model (GLM) with quasibinomial error structure. This approach was necessary because fruit set (the measure of reproductive success) is a binomial variable (it takes values between 0 and 1) and samples were not uniformly distributed within this interval (in several populations most plants had fruit sets close to 0); quasibinomial models take into account such overdispersion in the data. The relationship between distance to the apiary and fruit set was also evaluated using a quasibinomial GLM. GLMs were implemented in the R Statistical Environment (R Core Team, 2013).

Results

Reproductive success varied considerably both among sites and among years within specific sites (Table 3). Average fructification rate was under 10% in Učka and Keszthely, between 10–20% in Letaj, little above 20% in Sümeg and Paz, little above 30% in Kőszeg and outstandingly high (61.7%) at Nagytevel in 2013. The number of flowering individuals was not associated with the measured reproductive success, but the largest population (Učka) had the lowest fruit set.

The average reproductive success of the *H. adriaticum* population at Nagytevel in 2013 was significantly higher than in other population studied by us (both 2013 and earlier years), with three exceptions: Nagytevel 2010, Keszthely 2004 and Sümeg 2003 (Table 4).

The importance of apiaries in the pollination of Lizard Orchids is also shown by our observation that individual reproductive success in the population at Nagytevel decreased significantly with increasing distance from the apiary (quasibinomial GLM $F_{1,39}=18.52$, $p<0.001$, Fig. 1.).

Table 3. Reproductive success of populations studied in 2013 and in earlier years. *n*: total number of undamaged fruiting shoots observed in a given population.

Locality	Year	n	No. of flowers	No. of fruits	Fructification rate (%)
Nagytevel	2013	41	1477	911	61.7
Kőszeg	2013	36	1256	396	31.5
Sümeg	2013	54	1657	356	21.5
Keszthely	2013	32	1105	105	9.5
Učka	2013	100	2965	259	8.7
Letaj I.	2013	16	462	64	13.9
Letaj II.	2013	12	422	77	18.2
Paz	2013	7	210	44	21
Nagytevel	2010	11	227	118	52
Nagytevel	2011	41	1101	166	15.1
Sümeg	2002	76	2326	633	27.2
Sümeg	2003	19	486	256	52.7
Sümeg	2008	32	1009	242	24
Sümeg	2009	29	849	358	42.2
Sümeg	2010	25	640	179	28
Sümeg	2011	49	1337	281	21
Kőszeg	2010	33	1300	549	42.2
Kőszeg	2011	18	406	92	22.7
Keszthely	1992	25	909	171	18.8
Keszthely	1993	17	544	51	9.4
Keszthely	1994	19	671	36	5.4
Keszthely	1995	73	2758	219	7.9
Keszthely	1996	67	2130	342	16.1
Keszthely	1997	23	686	58	8.5
Keszthely	1998	30	975	197	20.2
Keszthely	1999	31	971	96	9.9
Keszthely	2000	12	333	19	5.7
Keszthely	2001	10	315	21	6.7
Keszthely	2002	32	912	156	17.1
Keszthely	2003	19	642	161	25.1
Keszthely	2004	20	524	286	54.6
Keszthely	2005	55	1736	297	17.1
Keszthely	2006	21	601	207	34.4
Keszthely	2007	21	530	187	35.3
Keszthely	2008	33	1040	128	12.3
Keszthely	2009	23	579	61	10.5
Keszthely	2010	12	267	10	3.7
Keszthely	2011	29	738	61	8.3

Discussion

The average reproductive success of the studied Lizard orchid populations was independent of the size of the population. A similar phenomenon was detected in the case of another nectarless orchid, *Orchis mascula*, where fruit set was low even in large populations in highly fragmented calcareous grassland in southern Belgium (Meekers and Honnay, 2011). In that area the percentage fruit set of same species was

independent from population size in undisturbed woodland but strongly related to population size in coppiced woodland (Jacquemyn et al., 2008). Fruit set was positively related to population size in the nectar producing *Gymnadenia conopsea* too (Meekers and Honnay, 2011). In contrast definitely reduced fecundity was observed in large populations of a nectar-rewarding species, *Spiranthes spiralis* (Petanidou et al., 2013). Fruit set in small populations of non-rewarding *Orchis purpurea* increased with population size (and decreased with increasing nearest-neighbour distance) (Jacquemyn et al., 2002).

Table 4. Parameter estimates, their standard errors, t-values and significance levels from the quasibinomial GLM comparing reproductive success of the Nagytevel 2013 population (the intercept of the model) to other samples. Reproductive success was significantly lower in other populations / years, except for the Keszthely 2004, Nagytevel 2010 and Sümeg 2003 samples.

Locality / Year	Estimate	Standard Error	t value	p value
Letaj II.-2013	-1.976	0.353	-5.603	0.000
Paz-2013	-1.804	0.458	-3.940	0.000
Letaj I.-2013	-2.304	0.373	-6.173	0.000
Učka-2013	-2.303	0.194	-11.857	0.000
Keszthely-2013	-2.730	0.298	-9.162	0.000
Sümeg-2013	-1.779	0.198	-9.008	0.000
Kőszeg-2013	-0.429	0.215	-2.000	0.046
Keszthely-1992	-1.938	0.258	-7.502	0.000
Keszthely-1993	-2.745	0.403	-6.810	0.000
Keszthely-1994	-3.346	0.462	-7.240	0.000
Keszthely-1995	-2.685	0.214	-12.524	0.000
Keszthely-1996	-1.931	0.198	-9.743	0.000
Keszthely-1997	-2.858	0.379	-7.535	0.000
Keszthely-1998	-1.849	0.247	-7.478	0.000
Keszthely-1999	-2.686	0.309	-8.685	0.000
Keszthely-2000	-3.281	0.624	-5.260	0.000
Keszthely-2001	-3.115	0.598	-5.212	0.000
Keszthely-2002	-2.054	0.265	-7.749	0.000
Keszthely-2003	-1.570	0.272	-5.775	0.000
Keszthely-2004	-0.292	0.265	-1.104	0.270
Keszthely-2005	-2.054	0.214	-9.584	0.000
Keszthely-2006	-1.120	0.260	-4.298	0.000
Keszthely-2007	-1.083	0.272	-3.986	0.000
Keszthely-2008	-2.440	0.279	-8.732	0.000
Keszthely-2009	-2.615	0.375	-6.977	0.000
Keszthely-2010	-3.722	0.841	-4.425	0.000
Keszthely-2011	-2.883	0.371	-7.775	0.000
Kőszeg-2010	-0.789	0.200	-3.951	0.000
Kőszeg-2011	-1.704	0.335	-5.086	0.000
Nagytevel-2010	-0.397	0.369	-1.075	0.282
Nagytevel-2011	-2.205	0.257	-8.579	0.000
Sümeg-2002	-1.024	0.177	-5.791	0.000
Sümeg-2003	-0.369	0.272	-1.359	0.175
Sümeg-2008	-1.629	0.235	-6.946	0.000
Sümeg-2009	-0.792	0.226	-3.506	0.000
Sümeg-2010	-1.422	0.265	-5.359	0.000
Sümeg-2011	-1.800	0.221	-8.142	0.000

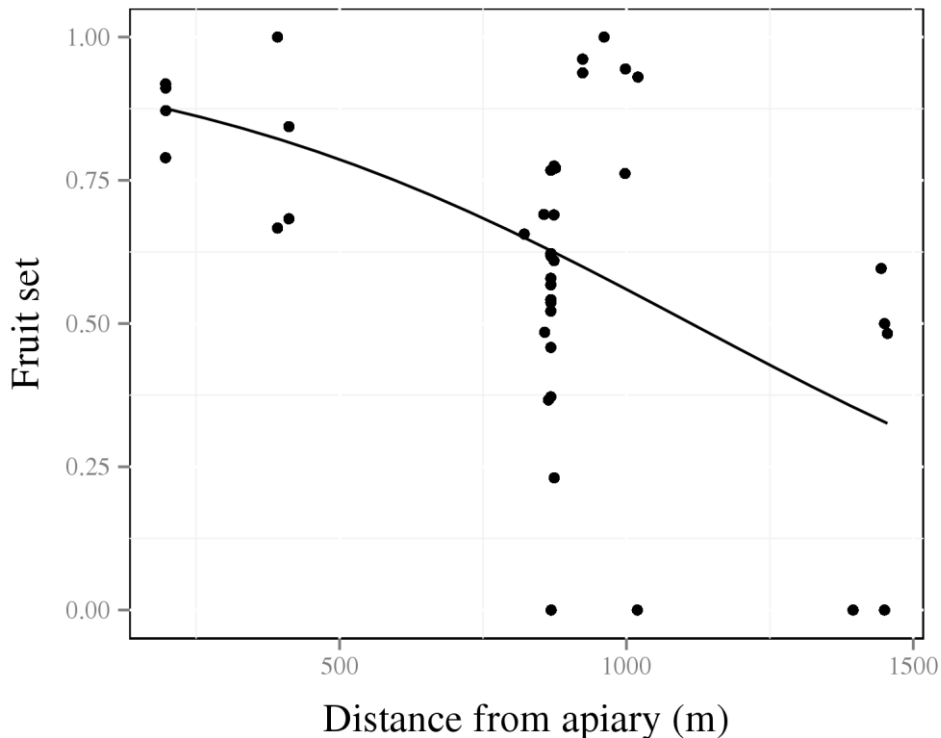


Figure 1. Relationship between individual distance from apiary and fruit set in Adriatic Lizard Orchids at Nagytevel (2013).

The realised 61.7% fructification rate in Nagytevel is the highest ever published population-level average reproductive success of *H. adriaticum*, although this was not significantly higher than the 52–54.6% reproductive success observed in three other populations in Hungary during earlier years. Overall average fruit set values of nectarless and nectariferous European orchids are 28% and 63%, respectively (Neiland and Wilcock, 1999) implying that the *Himantoglossum* population at Nagytevel reached the average fructification level of rewarding orchids.

Our results also show that the reproductive success of individual flowers in this population was negatively related to their distance from the beehives. Together, these results strongly suggest that honeybees were causally implicated in the high reproductive success of this population in 2013. Abundance of flower visiting honeybees depends on the distance from the nearest apiary in agricultural landscapes (Steffan-Dewenter and Tschardtke, 1999). Because the diversity of pollinators declines rapidly, the role of honeybees in pollination increases strongly (Brown and Paxton, 2009; Potts et al., 2010).

Frequent pollinators of *H. adriaticum* include both social (*Bombus* spp.) and solitary bees (*Andrena* spp., *Colletes similis*, *Osmia caerulescens*, *Megachile melanopyga*, *Lasioglossum* spp.). These are common species and forage on a wide variety of plant species. In arable field-margins in western France the most common pollinator species were *Andrena* and *Lasioglossum* (Féon et al., 2013), while near Göttingen in Germany, in an intensively managed agricultural landscape with islands of semi-natural calcareous grasslands *Osmia* and *Megachile* bee species were common pollinators (Steffan-Dewenter and Tschardtke, 2000).

Bee and insect-pollinated plant species richness was highest in Hungary when compared to Switzerland and the Netherlands. The richness of insect-pollinated plants is a good predictor of bee species richness across large geographic scales (Batáry et al., 2010).

Despite of relatively high species richness of bees and flowering plants in Hungary the pollination effect of honeybees was significant in Nagytevel. We can not exclude, however, that the earlier high fruit set data from Hungary were caused by honeybees. On the one hand average bee density is continuously increasing in Hungary: there were 7.78 honeybee colonies/km² in 1992 and 12.18 in 2012. On the other hand average bee density can strongly vary regionally (Tóth, 2013).

According to published data, honeybees are common pollinators of 21 food-deceptive and 12 nectar rewarding European terrestrial orchids (Table 5), mostly from the genera *Anacamptis* and *Orchis* (6–6 species), *Dactylorhiza* (5 species), *Epipactis*, *Gymnadenia* and *Himantoglossum* (3–3 species).

Table 5. Literature data about pollination European orchids by honeybees.

Species	Pollination	Source
<i>Anacamptis boryi</i>	Food-deceptive	Gumbert and Kunze 2001
<i>Anacamptis coriophora</i>	Nectar rewarding	Berger 2004
<i>Anacamptis coriophora</i> subsp. <i>fragrans</i>	Nectar rewarding	Peisl and Forster 1975
<i>Anacamptis morio</i>	Food-deceptive	Darwin 1877
<i>Anacamptis palustris</i>	Food-deceptive	Sulyok in Molnár 2011
<i>Anacamptis papilionacea</i>	Food-deceptive	Vöth 1989a
<i>Anacamptis pyramidalis</i>	Food-deceptive	Vöth 1999
<i>Dactylorhiza fuchsii</i>	Food-deceptive	Reinhard et al. 1991
<i>Dactylorhiza ochroleuca</i>	Food-deceptive	Bournérias and Prat 2005
<i>Dactylorhiza sambucina</i>	Food-deceptive	Nilsson 1980
<i>Dactylorhiza sphagnicola</i>	Food-deceptive	Claessens and Kleynen 2011
<i>Dactylorhiza sudetica</i>	Food-deceptive	Berger 2005
<i>Epipactis atrorubens</i>	Nectar rewarding	Wiefelspütz 1970
<i>Epipactis helleborine</i>	Nectar rewarding	Müller 1988
<i>Epipactis palustris</i>	Nectar rewarding	Darwin 1877
<i>Goodyera repens</i>	Nectar rewarding	Claessens and Kleynen 2013
<i>Gymnadenia corneliana</i>	Nectar rewarding	Berger 2009
<i>Gymnadenia lithopolitanica</i>	Nectar rewarding	Vöth 2000
<i>Gymnadenia nigra</i> s.l.	Nectar rewarding	Godfrey 1933
<i>Himantoglossum jankae</i>	Food-deceptive	Teschner 1980
<i>Himantoglossum adriaticum</i>	Food-deceptive	Vöth 1990
<i>Neotinea tridentata</i>	Food-deceptive	Vöth 1989b
<i>Neottia ovata</i>	Nectar rewarding	Nilsson 1981
<i>Orchis italica</i>	Food-deceptive	Vöth 1998
<i>Orchis mascula</i>	Food-deceptive	Darwin 1877
<i>Orchis militaris</i>	Food-deceptive	Vöth 1999
<i>Orchis ovalis</i>	Food-deceptive	Vöth 1999
<i>Orchis purpurea</i>	Food-deceptive	Godfrey 1933
<i>Orchis simia</i>	Food-deceptive	Godfrey 1933
<i>Spiranthes romanzoffiana</i>	Nectar rewarding	Larson and Larson 1987
<i>Spiranthes spiralis</i>	Nectar rewarding	Petanidou et al. 2013
<i>Traunsteinera globosa</i>	Food-deceptive	Vöth 1994

Based on our findings the practical application of apiaries in orchid conservation (for increasing reproductive success) seems to be promising, especially in the case of

deceptive orchids, which are characterized by a low flower visitation rate by pollinators and therefore by a low fruit set.

On the one hand, honeybees have been assumed to be superior competitors because of the high nectar and pollen requirements of their large perennial colonies compared to solitary bees. Furthermore they are believed to rapidly exploit rich patches of flowering plants using their dance language to communicate direction and distance of food resources to other foragers (Frisch, 1965; Visscher and Seeley, 1982; Beekman and Ratnieks, 2000). On the other hand, apiculture does not appear to have a negative impact on wild bees: neither species richness nor abundance of wild bees was negatively correlated with the density of honeybee colonies (within a radius of 2 km) or the density of flower-visiting honeybees per site despite the assumed competition between them (Steffan-Dewenter and Tschardt, 2000). The positive impact of increased honeybee amounts to the reproductive success of wild plants is not always well supported by empirical data (Klein et al., 2007). Our results based on reproductive success of deceptively pollinated orchid are confirming those opinions, that honeybees apart from being among the most important pollinators of agricultural crops, they also provide important pollination services to wild plants.

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