

1 **This manuscript is contextually identical with the following published paper:**
2 Sonkoly J; E.Vojtkó A; Tökölyi J; Török P; Sramkó G; Illyés Z; Molnár V.A. (2016) Higher
3 seed number compensates for lower fruit set in deceptive orchids. Journal of Ecology 104 (2)
4 pp. 343-351. DOI: 10.1111/1365-2745.12511
5

6 STANDARD PAPER

7 **Higher seed number compensates for lower fruit-set in deceptive orchids**

8 Running title: Seed production of orchids

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1 **Summary**

2 1. Floral deception is widespread in orchids, with more than one third of the species being
3 pollinated this way. The evolutionary success of deceptive orchids is puzzling, as species
4 employing this strategy are thought to have low reproductive success (less flowers yielding
5 fruits) because of low pollination rates. However, direct measurements of seed production in
6 orchids are scarce due to the extremely small size of their seeds.

7 2. Here, we quantified seed numbers in 1,015 fruits belonging to 48 orchid species from the
8 Pannonian ecoregion (central Europe) and obtained fruit-set and thousand-seed weight data
9 for these species from the literature. We used phylogenetic comparative methods to test the
10 hypothesis that deceptive species should compensate for their lower fruit-set by having either
11 larger seeds or more seeds in a fruit.

12 3. Similarly to previous studies, we found that deceptive orchids have substantially lower
13 fruits-set than nectar-rewarding ones. Also, we found that deceptive species have more seeds
14 in a fruit but not larger seeds compared to nectar-rewarding ones. Based on our results,
15 deceptive species compensate for their lower fruit-set by having higher seed numbers per
16 fruit, thus their seed numbers per shoot do not differ from that of nectar-rewarding ones.

17 4. Together with other benefits of deceptive pollination (e.g. lower energy expenditure due to
18 the lack of nectar production and higher genetic variability due to decreased probability of
19 geitonogamous pollination), our results can explain why deceptive strategies are so
20 widespread in the orchid family.

21 5. *Synthesis*. Our study provides new seed number data for 48 terrestrial orchid species.
22 Using these data we have tested the hypothesis that deceptive species should compensate for
23 their lower fruit-set by having either larger seeds or more seeds in a fruit than nectar-
24 rewarding ones. Our results suggest that deceptive species have more seeds in a fruit but not
25 larger seeds compared to nectar-rewarding ones. As a consequence, there are no significant

1 differences in seed numbers per shoot between different pollination types.

2

3 **Key-words:** deception, nectar-reward, Orchidaceae, phylogenetic control, reproductive

4 success, seed mass, seed number, thousand-seed weight, growth habit, **subject category**

5 **selected upon submission**

1 **Introduction**

2 Reproduction in plants requires transfer of pollen from male to female parts, which is often
3 achieved by enlisting animal pollinators, such as insects, bats or birds (Stpiczyńska 2003).
4 Most plants attract pollinators by supplying them with food, typically nectar and/or pollen.
5 Some plants, however, do not provide any reward but rely on deception, e.g. by mimicking
6 the flowers of nectar-rewarding species or the females of insect pollinators. Floral deception
7 evolved independently in at least 32 angiosperm plant families (Renner 2006) and is
8 especially common in orchids, where more than one third of the species (>6500 species) is
9 pollinated deceptively (Girord *et al.* 2002). Possible reasons for deception being
10 disproportionately frequent in the orchid family compared to other angiosperm families have
11 been assessed by Jersáková, Johnson & Kindlmann (2006). Within orchids, deceptive
12 pollination evolved multiple times independently, which might have played a key role in their
13 extraordinary diversification (Papadopoulos *et al.* 2013).

14 Known deception mechanisms in orchids involve food-deception, brood site imitation,
15 shelter imitation, pseudoantagonism, rendezvous attraction and sexual deception (Jersáková,
16 Johnson & Kindlmann 2006). The most common floral deception among orchids is food-
17 deception, where flowers resemble nectar-producing flowers (brightly coloured floral parts,
18 sweet smelling fragrances), but do not produce any nectar. Sexual deception is also quite
19 frequent, where flowers mimic the chemical signals, visual appearance and tactile perception
20 of female insects (mostly Hymenopterans), signals that attract males. Deceptive orchids
21 mostly rely on naive pollinators, since insects quickly learn to identify non-rewarding flowers
22 (Ferdy *et al.* 1998). As a consequence, pollination success in deceptive orchids is substantially
23 lower than in nectar-rewarding ones. According to Neiland & Wilcock (1998) the mean fruit-
24 set (the proportion of flowers that develop into fruits) of non-rewarding species in Europe is
25 27.7%, which is significantly lower than the mean fruit-set of rewarding species, 63.1%.

1 Tremblay *et al.* (2005) compared fruit-set data of both temperate and tropical orchid species,
2 and, consistently with the former results, found a significant difference between the mean
3 fruit-set of rewarding and non-rewarding species (37.1% and 20.7%, respectively). This low
4 pollination success is generally attributed to pollinator limitation (Alexandersson & Ågren
5 | 1996; Tremblay *et al.* 2005; Petanidou *et al.* 2013), although, resource limitation may play a
6 role as well, at least under certain circumstances (Ackerman & Montalvo 1990; Mattila &
7 Kuitunen 2000).

8 The evolutionary success of deceptive orchids is surprising in face of their reduced
9 reproductive success and is generally explained by two, mutually non-exclusive hypotheses
10 (Jersáková, Johnson & Kindlmann 2006). First, instead of nectar production, the plant might
11 allocate resources directly to reproduction, i.e. to fruit and seed production. The fact that
12 nectar production can consume a relevant proportion of resources during the flowering period
13 (Southwick 1984) and that nectar is often reabsorbed after pollination (Luyt & Johnson 2002;
14 Stpiczyńska 2003) and presumably diverted to fruit production supports the hypothesis that
15 producing nectar is costly. Second, nectarless flowers decrease the chance of pollinator-
16 mediated geitonogamy (pollination by pollen from another flower on the same plant), as
17 pollinators visit fewer flowers on the same plant if it is deceptive, thus enhancing outcrossing.
18 Accordingly, experimental evidence shows that adding artificial nectar to the spurs of non-
19 rewarding flowers increases the level of self-pollination and the proportion of removed
20 pollinia involved in self-pollination through geitonogamy (Johnson & Nilsson 1999; Johnson,
21 Peter & Ågren 2004; Jersáková, Johnson & Kindlmann 2006).

22 The above inference is based on the assumption that low pollination success results in
23 reduced reproductive success, since fruit-set is generally used as the sole measure of
24 reproductive success in orchids (Neiland & Wilcock 1998; Kull 2002). However, low
25 pollination success might be compensated by at least two mechanisms: (i) producing larger

1 seeds or (ii) producing more seeds per fruit. This 'compensation hypothesis' has not been
2 evaluated to date, partly because of methodological reasons: orchids have extremely light dust
3 seeds produced in very high numbers (Van der Pijl 1982; Arditti & Ghani 2000) and the
4 unusually high number of minute and low-weight seeds causes difficulties in the estimation of
5 seed production (Proctor & Harder 1994; Nazarov 1998). Due to these methodological
6 limitations, very few data have been published on the seed production of orchids. Seed
7 number data of only 17 European species were published by Arditti & Ghani (2000), but due
8 to the insufficient amount of data even basic descriptive statistics (mean and SD) were
9 impossible to calculate for many species.

10 Here we present data on the seed production of 48 central European terrestrial orchids
11 based on a high number of samples. We used this data to evaluate the 'compensation
12 hypothesis', which predicts that, if compensation for reduced fruit-set occurs in deceptive
13 orchids, these species should have larger seeds, and / or more seeds per fruit than nectar-
14 rewarding ones. To test this prediction, we compared species with different pollination types
15 in terms of seed size (thousand-seed weight, hereafter abbreviated as TSW) and capsular seed
16 number (seeds/fruit, hereafter abbreviated as CSN) using phylogenetic comparative methods.
17 Seed production of plants depends on a number of biotic and abiotic factors in general (e.g.
18 Leishman 2001; Moles *et al.* 2005a,b; Gundel *et al.* 2012), but little is known about the role of
19 these factors in shaping interspecific variation in seed size/number in orchids. To take into
20 account potentially confounding factors, we controlled for habitat shadiness (open or shady)
21 which has been shown to affect seed production (e.g. Nakagoshi 1985; Csontos 1998;
22 Milberg, Andersson & Thompson 2000; Fenner & Thompson 2005). We also controlled for
23 growth habit (tuberous or rhizomatous); as it may affect the amount of reserves stored in
24 below-ground organs, which can also affect reproduction.

1 **Materials and methods**

2 **Data collection**

3 We quantified CSN (capsular seed numbers) of a total of 1,015 fruits of 48 orchid taxa, which
4 is nearly three times the number of European species for which seed set data were available to
5 date (Arditti & Ghani 2000). Field sampling took place during 2009 and 2010 in several
6 locations across the Pannonian ecoregion (central Europe), during which fruits of 47 orchid
7 species were collected. We also collected mature, but intact fruits from herbarium specimens
8 in the herbarium of the Department of Botany, University of Debrecen (DE), which resulted
9 in fruit samples for 20 orchid species. In total we collected 22.9 ± 3.9 (mean \pm SE) fruits from
10 3.6 ± 0.4 (mean \pm SE) different locations per species. Undehisced fruits were usually collected
11 4–6 weeks after flowering.

12 Harvested fruits were stored in open Eppendorf tubes or scintillation vials depending
13 on their size. Fruits were left to dry on room temperature and were squashed by a metal
14 needle so that in every Eppendorf tube all seeds of the fruit and small parts of the pericarp
15 could be found. A known volume of glycerin (99.5%) was then pipetted into each tube and the
16 content was stirred by hand, using a metal needle (homogenization using a shaker was proved
17 to be unsatisfactory). In the highly viscous glycerin the very low density seeds rose to the
18 surface more slowly (several minutes) than in water (almost immediately). This allowed us to
19 make a suspension of seeds and then count the number of seeds in drops of glycerin as
20 follows. $10 \times 4 \mu\text{l}$ of the freshly stirred samples were pipetted onto object-slides and the
21 number of seeds in every drop was counted under a light microscope. The tip of the automatic
22 pipette tips ($1\text{--}10 \mu\text{l}$) were cut at an angle of cc. 45 degree in order to enable orchid seeds to
23 be imbibed. The number of seeds in a fruit was assessed based on the counted seed numbers
24 in the drops and the proportion of the drops to the whole volume.

25 To investigate whether the well-known difference between the fruit-set of deceptive

1 and nectar-rewarding species holds true for the studied species, we used fruit-set data
2 provided by Molnár V. (2011) mostly from Hungary, and in some cases (species for which
3 Hungarian data was not available) data from several European countries published by
4 Claessens & Kleynen (2011) (Table 1). To study whether deceptive species have larger seeds
5 TSW (thousand-seed weight) data were obtained from the database of Török *et al.* (2013).
6 Seed numbers per shoot (hereafter abbreviated as SNS) were obtained by multiplying the
7 mean capsular seed number of each species by the fruit number of the given species. Fruit
8 numbers are the means of multiple measurements done by Molnár V. (2011). (Note that fruit-
9 set and fruit number data used here were measured not just on the individuals from which
10 seed numbers originated, but on several other individuals too, thus these data are based on a
11 larger number of observations.)

12 To study the effect of pollination type on fruit-set, TSW, CSN and SNS, taxa were
13 categorized following Claessens & Kleynen (2011) (Table 1). We distinguished nectar-
14 rewarding, deceptive (food-deceptive and sexually deceptive) and autogamous groups. Both
15 facultative and obligate autogamy were considered as autogamy (self-pollination), as these
16 strategies both can be considered to be independent from pollinators (Molnár V. *et al.* 2012).
17 We controlled for habitat preference and growth habit, for which we distinguished species of
18 open habitats and species of shaded habitats, and rhizomatous and tuberous species according
19 to Kull & Hutchings (2006).

20

21 **Phylogenetic tree reconstruction**

22 In order to provide a phylogenetic framework for the studied species, we used sequences of
23 the nuclear ribosomal internal transcribed spacer (nrITS), one of the most heavily used
24 phylogenetic markers in species-level systematic studies (Baldwin *et al.* 1995; Álvarez &
25 Wendel 2003; Nieto-Feliner & Roselló 2007). The sequences were obtained – if available –

1 from GenBank, otherwise we either used the sequences of Bateman *et al.* (2003) or generated
2 the sequences newly. In this latter case, we used field-collected leaf samples dried in silica-
3 gel, and followed a modified CTAB-protocol to isolate total genomic DNA. The details of the
4 laboratory procedures for DNA-extraction and the amplification of the nrITS region are given
5 in more details in e.g. Sramkó *et al.* (2014). The successfully amplified samples were sent to
6 Macrogen Inc. (South-Korea) for Sanger-sequencing from the forward and reverse direction.
7 The sequences obtained were checked for intra-individual polymorphism (see Nieto-Feliner &
8 Roselló 2007); if an additive polymorphic site was detected, it was coded with IUPAC
9 ambiguity nucleotide codes (Cornish-Bowden 1985). All newly generated sequences were
10 uploaded to GenBank (for accession numbers see Table 1).

11 The nrITS region of our samples were aligned manually in BioEdit v.7.1.3 (Hall
12 1999), then the aligned matrix of 686 nucleotide length was used to reconstruct the
13 phylogenetic relationships of our studied species under the maximum parsimony (MP)
14 criterion in PAUP* v4.0b10 (Swofford 2003). Given the geographically limited sampling
15 (orchids of central Europe) for this study, there were evidently large gaps in our taxonomic
16 sample coverage for the phylogenetic work. Therefore, we used the well-established
17 molecular system of European orchids (Bateman *et al.* 2003; Bateman *et al.* 2005; Bateman
18 2009) as a backbone constraint (see Fig. 1) to fix the relationship between the main lineages
19 of the European orchids studied; and to avoid the potential drawback of a suboptimal
20 taxonomic sampling. Phylogenetic trees compatible with the above mentioned constraint were
21 searched in a heuristic way under the MP criterion in PAUP* applying all the default settings
22 but holding 10 trees in each iteration step and running 1000 random stepwise additions. The
23 root of the tree was specified by assigning the species of the Epidendroideae subfamily as
24 outgroup. To assess the robustness of our tree, we ran the non-parametric bootstrap test
25 (Felsenstein 1985) as implemented in PAUP* using 1000 pseudo-replications. Finally, one of

1 the most parsimonious trees with branch lengths was transformed to an ultrametric tree by the
2 non-parametric rate smoothing algorithm (Sanderson 1997) as implemented in r8s v.1.71
3 (Sanderson 2003). This procedure allowed us to generate branch lengths proportional to
4 genetic distance between the species, and the resulting ultrametric tree (Fig. 1) was used as
5 input for analyses using the phylogenetic control.

6

7 **Comparative analyses**

8 To study the relationship between orchid traits while controlling for phylogenetic relatedness,
9 we used Bayesian Phylogenetic Mixed Models (BPMs), as implemented in the
10 MCMCglmm package (Hadfield 2010), in the R Statistical Environment (R Core Team 2013).
11 BPMs are similar to traditional linear mixed models with the important difference that they
12 can incorporate hierarchical random effects arising e.g. from pedigrees or phylogenetic trees.
13 In this way, the non-independence of data points arising from shared phylogenetic descent of
14 taxa can be taken into account when evaluating the relationship between traits.

15 To test our hypothesis we built a full model that contained pollination type and
16 potential confounding factors, i.e. habitat preference and growth habit. We also used a
17 reduced model which contained only pollination type. We applied both models to analyze
18 fruit-set, TSW, CSN and SNS using the species-level dataset (i.e. data points were individual
19 taxa, as seen in Table 1). (Note that analyzing CSN on the individual level resulted in
20 essentially identical results; see S1 in Supporting Information). CSN and SNS were log-
21 transformed to obtain a normal distribution, and BPMs with Gaussian error structure were
22 employed. Fruit-set (which was a proportion variable) was analyzed using binomial BPMs
23 with the number of fruits (successes) and the number of unfertilized flowers (failures) as a
24 bivariate response. To account for overdispersion, an observation level random effect was
25 added to this model (Harrison 2014).

1 All models were run for 550,000 MCMC iterations, using a burn-in of 5,000 iterations
2 and a thinning interval of 500 iterations. We used parameter-expanded priors for the random
3 effects (MCMCglmm code: $V = 1$, $\nu = 0.002$). All models were run multiple times ($N > 3$)
4 and MCMC chains were visually checked to ensure that convergence was achieved.

1 **Results**

2 **Phylogenetic tree reconstruction**

3 We reconstructed the phylogenetic relationship between our studied species using a
4 constrained phylogenetic tree search under the MP criterion to provide measures of
5 phylogenetic relatedness. The heuristic search with 1000 random replicates found in 997
6 instances the same 28 equally most parsimonious trees. Between the trees found, the position
7 of the micro-species of *Epipactis helleborine sensu lato* and some notoriously problematic
8 species pairs (e.g. *Orchis militaris* and *O. purpurea*) were incongruent. These branches
9 received no (<50%) or low (<75%) statistical support in the non-parametric bootstrap
10 procedure (Fig. 1), otherwise our trees are compatible with the established phylogenetic
11 relationship of European orchids (Bateman *et al.* 2003; Bateman *et al.* 2005; Bateman 2009).
12 Thus, we selected one of the 28 trees (see Fig. 1) to represent the phylogenetic relatedness
13 between our samples, and this was made ultrametric for the subsequent analyses applying
14 phylogenetic control.

15

16 **Testing the 'compensation hypothesis'**

17 We calculated the CSN of 48 orchid species, CSN ranged from 910 to a maximum of 19,726
18 (Table 1). The highest CSN was recorded for deceptive species, whereas the lowest was found
19 for nectar-rewarding ones (Fig. 2). We calculated the SNS of 47 orchid species (for which
20 average fruit numbers were available). SNS ranged from 4,379 to 178,710 (Table 1). The
21 highest SNS was recorded for deceptive species, whereas the lowest was found for
22 autogamous ones (Fig. 2).

23 Pollination type had a significant effect on fruit-set: the fruit-set of deceptive species
24 was found to be significantly lower than that of nectar-rewarding ones (Table 2). Pollination
25 type had no effect on TSW, but significantly affected CSN, as CSN of deceptive species was

1 found to be significantly higher than that of nectar-rewarding ones (Table 2). We also
2 analysed the effect of pollination type on SNS, but we found no difference between the SNS
3 of different pollination types. Autogamous species did not differ significantly from nectar-
4 rewarding ones regarding any of the four studied variables (see Table 2 and Fig. 2). Habitat
5 preference and growth habit had no effect on any of the studied variables (Table 2).

1 **Discussion**

2 Earlier studies demonstrated that pollination type plays an important role in the life of
3 orchids; for instance it affects the intensity and frequency of pollination (Calvo 1993),
4 specific flowering time and vertical distribution (Pelissier *et al.* 2010) and climatic
5 responsiveness (Molnár V. *et al.* 2012). Additionally, as Neiland & Wilcock (1998) previously
6 noted, there is a strong connection between pollination type and fruit-set: nectar-rewarding
7 orchids have higher fruit-set compared to nectarless ones, which is clearly indicated by our
8 dataset as well. This difference is often considered to be a negative consequence of deceptive
9 pollination but, our results suggest that deceptive orchids can compensate for their lower fruit-
10 set by having more (but not larger) seeds in their fruits. However, higher capsular seed
11 numbers did not implicate significant differences in total number of seeds per shoot between
12 orchids with nectar-rewarding and deceptive entomophilous pollination.

13 According to this finding, we can say that fruit-set in itself is not sufficient to evaluate
14 the reproductive success of orchids, and reproductive success of deceptive species is not
15 necessarily lower than that of nectar-rewarding ones. This may explain results like that of
16 Jacquemyn *et al.* (2005), who have found that, despite their higher fruit-set, nectar-rewarding
17 orchids are not less threatened by local extinction and distribution decline than deceptive
18 ones. We are aware of the fact that even more factors (such as germination potential, seedling
19 establishment etc.) can be involved in reproductive success. However, since even the *in vitro*
20 estimation of germinability of orchid seeds is difficult to carry out (Vujanovic *et al.* 2000),
21 and there is little information on how *in vitro* and *in vivo* processes relate to each other (but
22 see e.g. Rasmussen *et al.* 1993), SNS can be the best and easiest approximation for orchids'
23 reproductive success to date.

24 A difference between temperate and tropical orchids similar to that between nectar-
25 rewarding and deceptive species was demonstrated by Neiland & Wilcock (1998): they stated

1 that tropical species are only about one-third as successful as temperate ones, based on their
2 average fruit-set values (13.6% and 38.2%, respectively). Similarly to our hypothesis, they
3 also suggested that tropical orchids may compensate for their very low fruit-set by having
4 more seeds in a fruit, as they found that the nine tropical species for which Arditti & Ghani
5 (2000) provided seed number data have about 150 times more seeds in a fruit than the eight
6 temperate species. Although this result is based on a relatively small number of observations,
7 the parallelism between this and our result is remarkable.

8 Neiland & Wilcock (1998) suggested that despite being energetically demanding,
9 nectar production might be the most effective strategy to improve pollination success in the
10 Orchidaceae. Reproduction in deceptive orchids is usually considered to be severely
11 pollination limited (e.g. Calvo 1993; Tremblay *et al.* 2005), based on which, allocating
12 resources to nectar production to attract pollinators should be worthwhile. However, in
13 addition to being pollination limited, resource availability can also be an important limiting
14 factor, at least in certain species and years (Zimmerman & Aide 1989; Ackerman & Montalvo
15 1990). Our results may also underline the possible effect of resource limitation, as we found
16 that nectar-rewarding species have lowered CSN compared to deceptive species, which may
17 be the result of plants with more fruits being able to produce fewer seeds within a fruit, i.e.
18 resource limitation.

19 Larger seed size could also compensate for lower fruit-set, as in other plant species it
20 seems to positively affect germination (e.g. Eriksson 1999; Jakobsson & Eriksson 2000),
21 seedling establishment and performance (e.g. Moles *et al.* 2004; Baroloto, Forget & Goldberg
22 2005) and the subsequent growth and reproductive capacity of the plant (e.g. Stanton 1985;
23 Tremayne & Richards 2000). However, we did not find any difference between the TSW of
24 pollination types, thus, deceptive species did not seem to compensate for their lower fruit-set
25 by having larger seeds.

1 There are known benefits of deceptive pollination, such as (i) lower energy
2 expenditure due to the lack of nectar production and (ii) higher genetic variability due to
3 decreased probability of geitonogamous pollination (Jersáková, Johnson & Kindlmann 2006).
4 Jersáková, Johnson & Kindlmann (2006) also admitted that despite these benefits, it is hard to
5 explain the evolutionary stability of this strategy, as, at least when pollinators are scarce,
6 mutations for nectar production would spread through the whole population. However,
7 additionally to these known benefits, we found that CSN of deceptive species is higher than
8 that of nectar-rewarding ones and their SNS is similar to that of nectar-rewarding ones, which
9 may explain why deceptive strategies are so widespread in the orchid family.

10

11 **Acknowledgements**

12 Orsolya Vincze (University of Debrecen), Zoltán Barta (University of Debrecen). Jonathan
13 Mitchley (University of Reading) and János Podani (Eötvös Lóránd University) kindly
14 improved our English. We are also grateful to those colleagues who have uploaded the
15 sequences used in this study to GenBank. The work was financially supported by the
16 European Union and the State of Hungary, co-financed by the European Social Fund in the
17 framework of TÁMOP-4.2.4.A/2-11/1-2012-0001 ‘National Excellence Program’. The
18 instrumental and infrastructural support of OTKA Grants to A.M.V. (K108992), to P.T.
19 (PD100192) and G.S. (PD109686) is also highly appreciated

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1 **SUPPORTING INFORMATION**

2 Additional supporting information may be found in the online version of this article:

3

4 **Table S1.** Results of BPMMs on the effect of pollination type, habitat preference and growth
5 habit on capsular seed number (CSN) on the individual level.

6

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10 missing files) should be addressed to the authors.

1 **Table 1.** Characteristics of the 48 species studied. Codes: **FS** – fruit-set (%), as published by
2 Molnár V. (2011) and Claessens & Kleynen (2011); **TSW (g)** – thousand-seed weight (in
3 grams) – based on the dataset of Török *et al.* (2013) **CSN** – capsular seed number
4 (mean±SE); **n** – number of fruits studied; **L** – number of collecting localities; **FN** – average
5 number of fruits according to Molnár V. (2011); **SNS** – seed number per shoot; **Poll** –
6 pollination type: **A** – autogamous, **D** – deceptive, **NR** – nectar-rewarding; **Hab** – habitat
7 preference: **O** – open habitats, **F** – forest habitats; **GH** – growth habit: **T** – tuberous, **R** –
8 rhizomatous. *Measurements carried out for this study, following the methodology of Török
9 *et al.* (2013); ** Data from Ljubka *et al.* (2014).
10

Taxon	FS	TSW (g)	CSN	n	L	FN	SNS	Poll	Hab	GH	nrITS source (GenBank acc. no.)
<i>Anacamptis coriophora</i>	83.0	0.0024	3192±340	26	8	16.1	51257	NR	O	T	AY369086
<i>Anacamptis morio</i>	32.0	0.0010	4978±521	20	7	4.6	22926	D	O	T	AY364881
<i>Anacamptis palustris</i> agg.	62.2	0.0019	7379±535	38	1	9.0	66410	D	O	T	Generated for this study
<i>Anacamptis pyramidalis</i>	28.7	0.0016	2262±205	23	3	19.1	43282	D	O	T	AY364870
<i>Cephalanthera damasonium</i>	84.5	0.0028	4528±677	27	11	4.1	18631	A	F	R	AY146446
<i>Cephalanthera longifolia</i>	11.5	0.0040	4231±342	21	3	1.8	7687	D	F	R	AY146447
<i>Cephalanthera rubra</i>	13.8	n.d.	4725±840	12	4	0.9	4379	D	F	R	AY369084
<i>Dactylorhiza fuchsii</i>	75.9	0.0018	5205±914	27	2	16.9	87786	D	O	T	DQ022864
<i>Dactylorhiza incarnata</i> agg.	63.0	0.0025	7076±881	27	8	25.3	178710	D	O	T	DQ022885
<i>Dactylorhiza majalis</i>	34.0	0.0021	9639±421	62	1	10.9	105229	D	O	T	DQ074217
<i>Dactylorhiza sambucina</i>	18.8	n.d.	3014±168	85	2	5.5	16652	D	O	T	DQ074239
<i>Dactylorhiza viridis</i>	36.5	0.0022	1453±136	11	4	10.4	15157	NR	O	T	DQ022880
<i>Epipactis albensis</i>	75.5	0.0030**	5997±553	6	1	10.6	63570	A	F	R	Generated for this study
<i>Epipactis atrorubens</i>	75.2	0.0046	3226±618	7	4	14.4	46596	NR	F	R	FR750398
<i>Epipactis bugacensis</i>	77.8	0.0034	4142±1067	8	1	9.2	38188	A	F	R	Generated for this study
<i>Epipactis helleborine</i>	82.0	0.0024	6486±677	7	2	8.7	56518	NR	F	R	EF153104
<i>Epipactis leptochila</i>	78.6	n.d.	3154±280	9	1	10.0	31544	A	F	R	Generated for this study
<i>Epipactis mecsekensis</i>	76.8	0.0022	4266±391	4	1	7.4	31705	A	F	R	Generated for this study
<i>Epipactis microphylla</i>	74.0	0.0035	2729±379	8	3	6.1	16574	A	F	R	FR750399
<i>Epipactis neglecta</i>	81.6	0.0021	4761±901	8	2	1.1	5347	A	F	R	Generated for this study
<i>Epipactis nordeniorum</i>	80.1	0.0016	4636±669	8	2	9.2	42618	A	F	R	Generated for this study
<i>Epipactis palustris</i>	74.0	0.0030*	5750±690	11	6	9.6	55486	NR	O	R	AY146448
<i>Epipactis pontica</i>	68.4	0.0019	2651±309	6	3	5.8	15243	A	F	R	Generated for this study
<i>Epipactis tallosii</i>	75.4	0.0019	4121±354	13	4	10.8	44459	A	F	R	Generated for this study
<i>Epipactis voethii</i>	n.d.	0.0025	6102±1189	17	3	n.d.	n.d.	A	F	R	FR750400
<i>Goodyera repens</i>	73.9	0.0017	2509±224	10	1	8.8	22123	NR	F	R	HM021556
<i>Gymnadenia conopsea</i>	80.3	0.0031	5005±782	34	12	27.5	137851	NR	O	T	DQ351281
<i>Gymnadenia odoratissima</i>	70.2	0.0017	1278±176	26	2	41.4	52924	NR	O	T	Generated for this study
<i>Himantoglossum adriaticum</i>	18.7	0.0013	10686±1550	22	3	12.7	136145	D	O	T	FR750401
<i>Himantoglossum jankae</i>	30.8	0.0006	12085±1124	29	3	9.4	113717	D	O	T	FR750402
<i>Limodorum abortivum</i>	82.8	0.0034	3623±808	9	4	8.3	30034	A	O	R	AY351378
<i>Liparis loselii</i>	57.9	n.d.	11354±587	14	2	9.3	105023	A	O	T	AJ551453
<i>Neotinea tridentata</i>	39.7	0.0015	6064±361	69	4	10.0	60806	D	O	T	Z94113-4
<i>Neotinea ustulata</i>	21.3	0.0010	2787±519	11	3	17.6	48949	D	O	T	FR750397
<i>Neottia nidus-avis</i>	87.1	0.0031	2774±303	24	4	25.4	70454	A	F	R	AY351383
<i>Neottia ovata</i>	44.0	n.d.	910±211	4	2	33.1	30104	A	F	R	FJ694841
<i>Ophrys apifera</i>	77.9	0.0011	8068±912	15	3	3.3	26949	A	O	T	AM980999
<i>Ophrys fuciflora</i>	17.3	0.0020*	5165±835	3	3	3.4	17769	D	O	T	AJ972932
<i>Ophrys oestrifera</i>	24.8	0.0017	19726±4189	8	2	1.4	27475	D	O	T	AM981015
<i>Ophrys sphegodes</i>	7.6	n.d.	16041±2097	27	9	1.6	26249	D	O	T	AJ973255
<i>Orchis militaris</i>	18.1	0.0014	10948±3274	9	4	10.8	118243	D	O	T	AY699977
<i>Orchis pallens</i>	31.6	0.0023*	6139±1393	8	1	6.3	38678	D	F	T	Generated for this study
<i>Orchis purpurea</i>	17.5	0.0016	7360±580	13	5	10.5	77565	D	O	T	AY364882
<i>Orchis simia</i>	37.2	0.0007	5780±355	34	2	9.2	52924	D	O	T	Z94107-8
<i>Platanthera bifolia</i>	69.9	0.0013	6146±325	99	12	12.6	77261	NR	F	T	Generated for this study
<i>Platanthera chlorantha</i>	79.8	0.0010	5295±650	11	1	6.8	35973	NR	F	T	Z94117-8
<i>Spiranthes spiralis</i>	58.7	n.d.	3527±383	6	2	18.8	66301	NR	O	T	FJ473354
<i>Traunsteinera globosa</i>	57.2	n.d.	2486±226	38	2	32.4	80438	D	O	T	Generated for this study

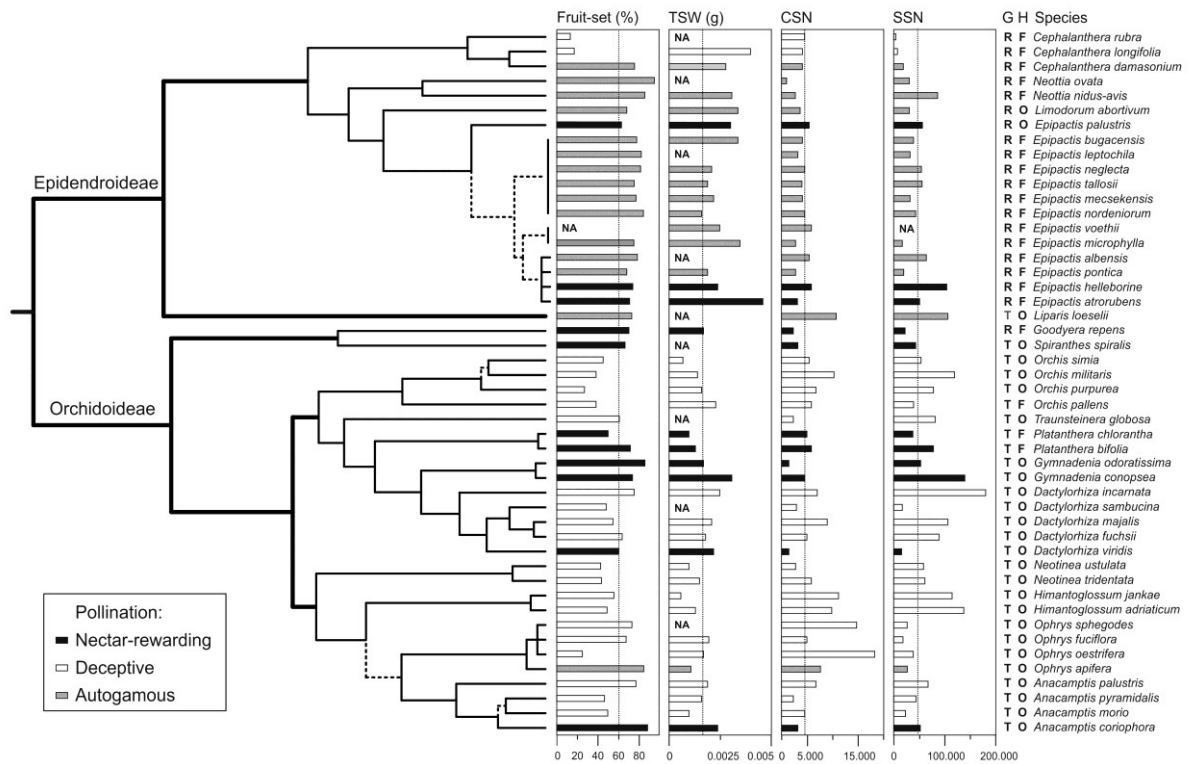
1 **Table 2.** Results of BPMMs on the effect of pollination type, habitat preference and growth
2 habit on the fruit-set, thousand-seed weight (TSW), capsular seed number (CSN) and seed
3 number per shoot (SSN) of species

Fruit-set	Full model				Reduced model			
Parameter	post.mean	l-95%	u-95%	pMCMC	post.mean	l-95%	u-95%	pMCMC
(Intercept)	0.962	-0.246	2.219	0.139	1.036	0.409	1.756	0.004 **
Pollination - Deceptive	-1.608	-2.336	-0.781	<9e-04 ***	-1.436	-2.226	-0.680	<9e-04 ***
Pollination - Autogamous	0.464	-0.396	1.350	0.306	0.321	-0.566	1.126	0.477
Habitat shadiness - Shady	-0.265	-1.191	0.632	0.582				
Growth habit - Tuberous	0.339	-0.806	1.517	0.591				

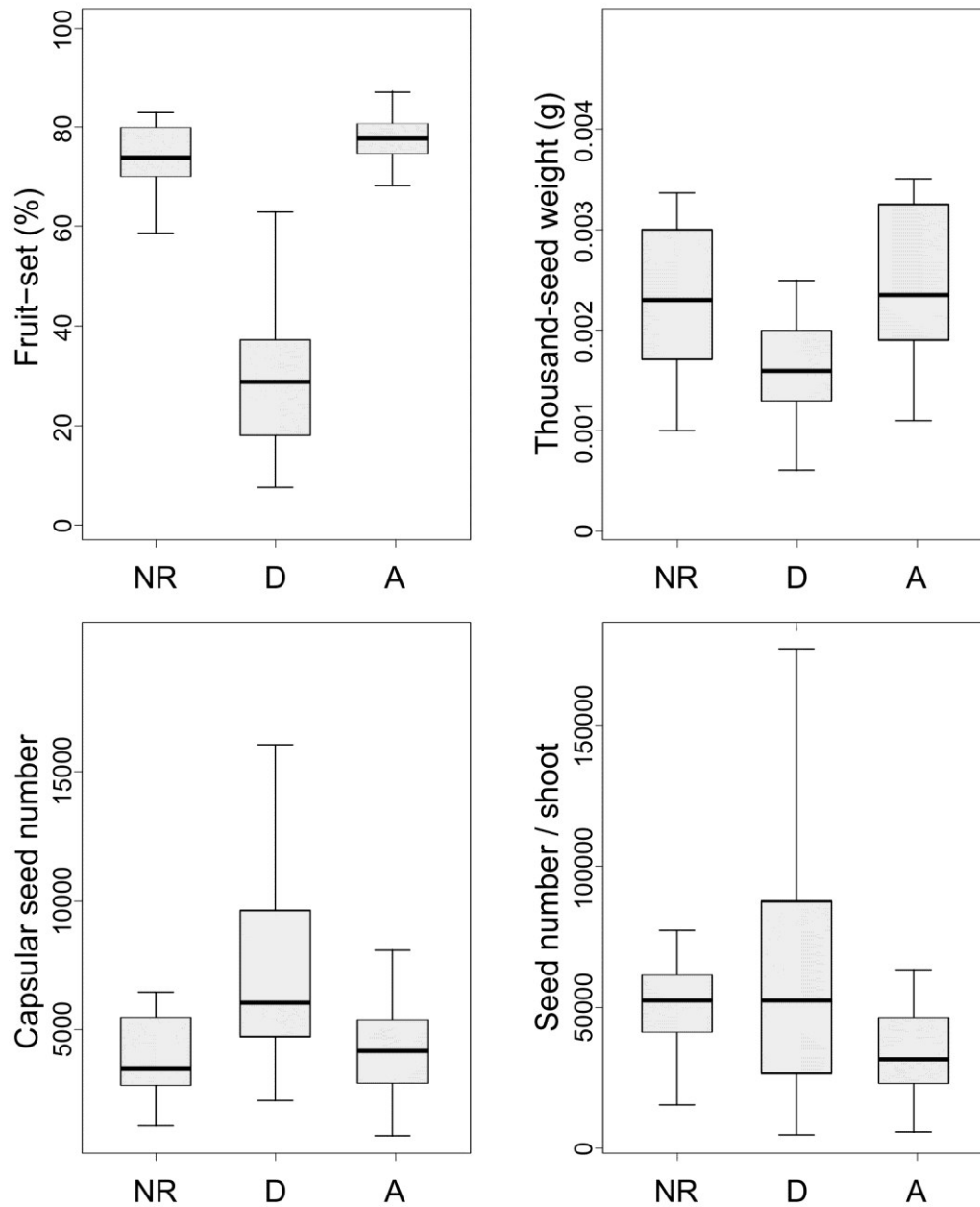
TSW	Full model				Reduced model			
Parameter	post.mean	l-95%	u-95%	pMCMC	post.mean	l-95%	u-95%	pMCMC
(Intercept)	0.003	-0.019	0.027	0.794	0.002	-0.012	0.021	0.780
Pollination - Deceptive	0.000	-0.009	0.012	0.976	-0.000	-0.011	0.009	0.939
Pollination - Autogamous	-0.001	-0.012	0.010	0.894	-0.001	-0.013	0.009	0.903
Habitat shadiness - Shady	-0.000	-0.012	0.013	0.998				
Growth habit - Tuberous	-0.001	-0.034	0.026	0.983				

CSN	Full model				Reduced model			
Parameter	post.mean	l-95%	u-95%	pMCMC	post.mean	l-95%	u-95%	pMCMC
(Intercept)	11.611	9.347	13.833	<9e-04 ***	12.293	10.85	13.759	<9e-04 ***
Pollination - Deceptive	0.968	-0.023	1.971	0.051	1.057	0.123	2.113	0.038 *
Pollination - Autogamous	0.226	-0.949	1.471	0.686	0.175	-0.874	1.343	0.745
Habitat shadiness - Shady	0.003	-1.132	1.348	0.987				
Growth habit - Tuberous	1.196	-1.188	3.562	0.294				

SSN	Full model				Reduced model			
Parameter	post.mean	l-95%	u-95%	pMCMC	post.mean	l-95%	u-95%	pMCMC
(Intercept)	10.524	9.318	11.645	<9e-04 ***	10.784	10.124	11.467	<9e-04 ***
Pollination - Deceptive	-0.213	-0.870	0.479	0.530	-0.101	-0.771	0.554	0.745
Pollination - Autogamous	-0.117	-0.839	0.627	0.780	-0.258	-0.985	0.455	0.468
Habitat shadiness - Shady	-0.065	-0.768	0.820	0.866				
Growth habit - Tuberous	0.492	-0.724	1.500	0.336				



1
2 **Fig. 1.** The favoured phylogenetic tree of 28 equally most parsimonious trees made
3 ultrametric by non-parametric rate smoothing and used in all subsequent analyses as
4 phylogenetic control. The backbone constraint applied in the heuristic MP search is indicated
5 by thick branches, whereas branches receiving low statistical support (50–75 %) in our
6 bootstrap analysis are dashed. Trait values for fruit-set, CSN, SSN, growth habit (GH) and
7 habitat preference (H) for each taxon are given next to the tree. Pollination type was indicated
8 with different colours of the bars.



1
2 **Fig. 2.** Fruit-set (%), thousand seed weight, capsular seed number and seed number per shoot
3 of orchids with different pollination types. Deceptive species have significantly lower fruit-set
4 but significantly higher capsular seed number compared to nectar-rewarding ones, and there
5 are no significant differences between the thousand-seed weight and seed number per shoot of
6 different pollination types.