

Does nectar reward affect rarity and extinction probabilities of orchid species? An assessment using historical records from Belgium and the Netherlands

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Abstract

The long-term persistence of plant populations may partly depend on pollination processes and seed production. The exact role of pollination in determining plant population viability still remains largely unclear. Orchid species have often been shown to be pollinator limited. Especially, non-rewarding species are characterized by infrequent pollinator visits and low seed set. Therefore, it can be hypothesized that, if overall population fitness of orchid species is influenced by seed production, non-rewarding species should be more prone to local extinction than rewarding species. To study the importance of nectar reward on orchid persistence, we collected historical records about the distribution of 32 orchid species in Flanders (Belgium) and 37 orchid species in the Netherlands. For both regions, present distribution patterns were compared with historical data. Between 1930 (Flanders) or 1950 (the Netherlands) and 2000, 26 (81%) species showed decreases in distribution range in Flanders, eight of which had gone extinct, whereas 29 (78%) species showed declines in distribution area in the Netherlands, five of which went extinct. Contrary to previously reported results, orchid distribution patterns were not related to nectar reward. There was also no significant relationship between nectar reward and extinction for both regions. Orchids typically occurring in wet grasslands and heathlands suffered greater losses than orchids typically confined to forest habitats or calcareous grasslands. We conclude that the production of nectar does not represent a safeguard for local extinction of orchid species. Habitat loss and other deterministic threats associated with habitat fragmentation and deterioration are more important determinants of orchid persistence.

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1. Introduction

Despite an increasing interest in plant–pollinator interactions (Kearns et al., 1998), the relative importance of pollination processes and seed production in determining population viability and long-term persistence of plant populations remains largely unexplored (Crawley, 1990; Menges, 2000). There is some evidence that in annuals and short-lived perennials a reduction in seed set due to a pollinator deficit may lead to decreased

population size and increased probabilities of extinction (Groom, 1998; Lennartsson, 2002). For the latter, it can be expected that successful pollination and seed set are most important as they may maintain or even enhance recruitment rates and consequently population growth rates. For long-lived perennials, however, the importance of seed set on overall population fitness may be less pronounced because population growth rates of these species generally depend more on growth and survival rates than on fecundity (Silvertown et al., 1993, 1996). However, when seed production and recruitment are severely limited, long-lived perennials may show negative growth rates too, as elasticity values for fecundity and population growth rates λ have been shown to be positively related (Oostermeijer et al., 1996;

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Caswell, 2001). As a result, populations characterized by reduced seed output and recruitment may slowly evolve to population structures characterized by a lack of recruits and a large proportion of (mostly old) adult individuals, and ultimately to local extinction (e.g. Jacquemyn et al., 2003; Brys et al., 2003).

Most orchid species are characterized by low pollination success and seed set (Neiland and Wilcock, 1998). Low seed set may result from resource limitation, pollinator limitation, or both (Willems and Lahtinen, 1997; Matilla and Kuitunen, 2000). It has been shown that especially non-rewarding species, which make up nearly one-third of all orchid species (Ackerman, 1986), have very low visitation frequencies of pollinators and as a consequence low levels of fruit set (Dafni and Ivri, 1979; Gill, 1989; Neiland and Wilcock, 1998). Pollination levels of less than 50% have been frequently observed among nectarless orchids, whereas nectariferous orchids mostly had pollination levels well above 50% (Neiland and Wilcock, 1998). Therefore, it can be hypothesized that, if overall population viability of especially non-rewarding orchid species is limited due to low seed set, nectar reward may be a causal factor determining orchid rarity (Darwin, 1862; Neiland and Wilcock, 1998).

On the other hand, it has been shown that fruit set of nectarless orchids is less severely affected by a reduced population size (i.e. the Allee effect) (Fritz and Nilsson, 1994; Oostermeijer et al., 2000), and as a consequence these species may be less susceptible to fragmentation processes. In contrast, nectariferous orchids are highly dependent on pollinators to reach their high reproductive success and therefore the latter may be more vulnerable to Allee effects following fragmentation. This leads to the alternative hypothesis that in severely fragmented landscapes like in Belgium and the Netherlands, nectariferous orchids may have shown higher extinction rates than nectarless species.

In this paper, we collected long-term historical data on distribution ranges of orchid species using distribution maps of 4×4 or 5×5 km² grid squares. To test hypotheses about the underlying mechanisms of orchid rarity and decline, we compared actual distribution patterns of orchid species with historical records from the 1930s and 1950s, respectively. To minimize the possibility of the mechanisms being dependent on the region studied, we collected data for two regions characterized by different abundances of orchid populations (Flanders and the Netherlands). The following hypotheses were tested in this study: (1) can differences between nectariferous and nectarless orchids explain differences in orchid rarity, as was suggested by Darwin (1862) and (2) given their dependency on pollinators to obtain a high reproductive success, are nectariferous orchid species more prone to extinction due to fragmentation processes than non-rewarding species?

2. Material and methods

2.1. Historical records and current distribution

To study temporal changes in population distribution and to investigate the importance of nectar reward in determining extinction rates of orchid species, historical data on species occurrence were compared with present distributions for 32 and 37 orchid species, in Flanders (Belgium) and the Netherlands, respectively. Changes in orchid distributions in Flanders were studied between 1930 and 2000 using a 4×4 km² grid and in the Netherlands between 1950 and 2000 using a 5×5 km² grid. For both regions, herbarium records and historical field data were used to identify populations that existed in the early 1930s and 1950s. For the Flanders data set, no historical data were available for the orchid species *Epipactis helleborine*, *Listera ovata* and *Goodyera repens*. Three species from the genus *Dactylorhiza* (*Dactylorhiza fuchsii*, *D. sphagnicola* and *D. maculata*) were considered as one group in the 1930 data and were therefore not included in the data set of Flanders. No data were available for *D. fuchsii*, *D. sphagnicola* and *D. praetermissa* for that of the Netherlands. Three species that did not establish spontaneously and have already disappeared again (*Orchis laxiflora*, *Ophrys sphegodes* and *O. fuciflora*) (Kreutz and Dekker, 2000), were also not included in the Netherlands data set. Data for the Netherlands were taken from Kreutz and Dekker (2000) and for Flanders from the Florabank database. Information on pollination systems and nectar production was acquired from van der Cingel (1995).

To determine whether changes in distribution range were related to habitat traits, orchid species were categorized in four major groups, according to their habitat preference: (1) species characteristic for calcareous grasslands, (2) species confined to forests and forest edges, (3) species mainly growing in wet grasslands and fens and (4) species generally occurring in heathlands and nutrient-poor grass heaths. A full list of all investigated species is given in Table 1.

2.2. Data analysis

To test the hypothesis that orchid rarity was related to nectar reward, we used the historical data rather than information on the current distribution area as the former may give a more accurate picture of the natural distribution patterns of orchids without the confounding effects of fragmentation and habitat loss. For each region, we calculated for each group (non-rewarding vs. rewarding): (1) the number of very rare species (i.e. species occurring in less than 0.5% of all grid cells), (2) the number of rare species (i.e. between 0.5% and 1.5% of all grid cells occupied), (3) the number of species with a restricted distribution area (i.e. between 1.5% and 5%

Table 1

List of the investigated species with their reproductive system and the habitats where they are typically found

	Rewarding species	Non-rewarding species
Calcareous grasslands	<i>Aceras anthropophorum</i> , <i>Gymnadenia conopsea</i> , <i>Himantoglossum hircinum</i> , <i>Orchis coriophora</i>	<i>Anacamptis pyramidalis</i> , <i>Ophrys apifera</i> , <i>O. fuciflora</i> , <i>O. sphegodes</i> , <i>Orchis militaris</i> , <i>O. ustulata</i>
Forests and forest edges	<i>Epipactis atrorubens</i> , <i>E. helleborine</i> , <i>E. muelleri</i> , <i>Goodyera repens</i> , <i>Listera cordata</i> , <i>L. ovata</i> , <i>Neottia nidus-avis</i> , <i>Platanthera chlorantha</i>	<i>Cephalanthera damasonium</i> , <i>C. longifolia</i> , <i>C. rubra</i> , <i>Corallorhiza trifida</i> , <i>Ophrys insectifera</i> , <i>Orchis mascula</i> , <i>O. purpurea</i> , <i>O. simia</i>
Wet grasslands and fens	<i>Epipactis palustris</i> , <i>Herminium monorchis</i>	<i>Dactylorhiza incarnata</i> , <i>D. majalis</i> , <i>D. praetermissa</i> , <i>Hammarbya paludosa</i> , <i>Liparis loeselii</i> , <i>Orchis palustris</i>
Heathlands and nutrient-poor grass heaths	<i>Coeloglossum viride</i> , <i>Platanthera bifolia</i> , <i>Pseudorchis albida</i> , <i>Spiranthes aestivalis</i> , <i>S. spiralis</i>	<i>Dactylorhiza maculata</i> , <i>Orchis morio</i>

of all grid cells occupied) and (4) the number of more or less 'wide-spread' species (species occurring in more than 5% of all grid cells). A two-way test of independence (G test with Williams's correction) was used to test whether the distribution patterns of non-rewarding species differed significantly from that of rewarding orchids.

To investigate whether orchid persistence was related to nectar reward, the historical and current data were compared. First, changes in distribution range were analysed by plotting the number of grid cells occupied by a species in 1930 or 1950 against the number of grid cells occupied in 2000. Analysis of covariance (ANCOVA) was used to determine whether the overall change in distribution range differed significantly from zero. The percentage change in the number of grid cells occupied by a species was calculated as $(N_e - N_s) / N_s \times 100$ where N_e is the number of grid cells occupied by a species in 2000 and N_s is the number of grid cells occupied in 1930. A Mann–Whitney U test was used to test the hypothesis that percentage changes in distribution area were related to nectar reward. We also tested the hypothesis that non-rewarding species were more prone to regional extinction than rewarding species by means of analysis of deviance of a logistic regression model. Significance was tested with a likelihood ratio test, which tests the change in deviance after including the dependent variable in the model. Deviance changes follow the χ^2 distribution. Finally, to test the hypothesis that changes in distribution range were related to the habitats they are confined to, non-parametric ANOVA (Kruskal–Wallis test) was used.

3. Results

3.1. Nectar reward and orchid rarity

For both regions (Flanders and the Netherlands), no association between nectar reward and orchid rarity was found ($G_{adj} = 2.49$, $df = 2$, $P = 0.29$ and $G_{adj} = 3.81$, $df = 3$, $P = 0.28$, respectively). For Flanders, there was a

Table 2

The number of rewarding and non-rewarding orchid species in Flanders, grouped according to their different rarity category for Flanders and the Netherlands

	Distribution				Total
	<0.5%	0.5–1.5%	1.5–5%	>5%	
<i>Flanders</i>					
Non-rewarding	10	5	3	–	18
Rewarding	4	5	5	–	16
<i>The Netherlands</i>					
Non-rewarding	5	6	1	6	18
Rewarding	6	3	5	5	19

tendency for a larger number of nectarless species with a very restricted distribution area (i.e. less than 0.5% of all grid cells occupied) (Table 2). For the Netherlands, however, no such trend was observed.

3.2. Changes in orchid distribution area

Comparison of the historical and current distribution area revealed that for both regions the distribution of most orchid species declined (Fig. 1(a) and (b)). For both regions, there was a significant difference in the slope between the regression line through the origin and the $y = x$ regression line, the latter indicating no change in distribution range between the two studied periods (analysis of covariance, $F = 34.8$, $P = 0.001$ and $F = 9.63$, $P = 0.003$, respectively). In the period 1930 (1950)–2000, the mean number of occupied grid cells declined from 10.8 to 5.6 (48%) in Flanders and from 105 to 66 (37%) in the Netherlands. Only six (19%) and 10 species (22%) were able to expand their range during the studied periods in Flanders and the Netherlands, respectively. Range expansion was most pronounced for *Dactylorhiza praetermissa*, *Ophrys apifera* and *Orchis militaris* in Flanders, and *Anacamptis pyramidalis* and *Ophrys apifera* in the Netherlands (Fig. 1(a) and (b)). The distribution area of *Himantoglossum hircinum* also increased in both regions.

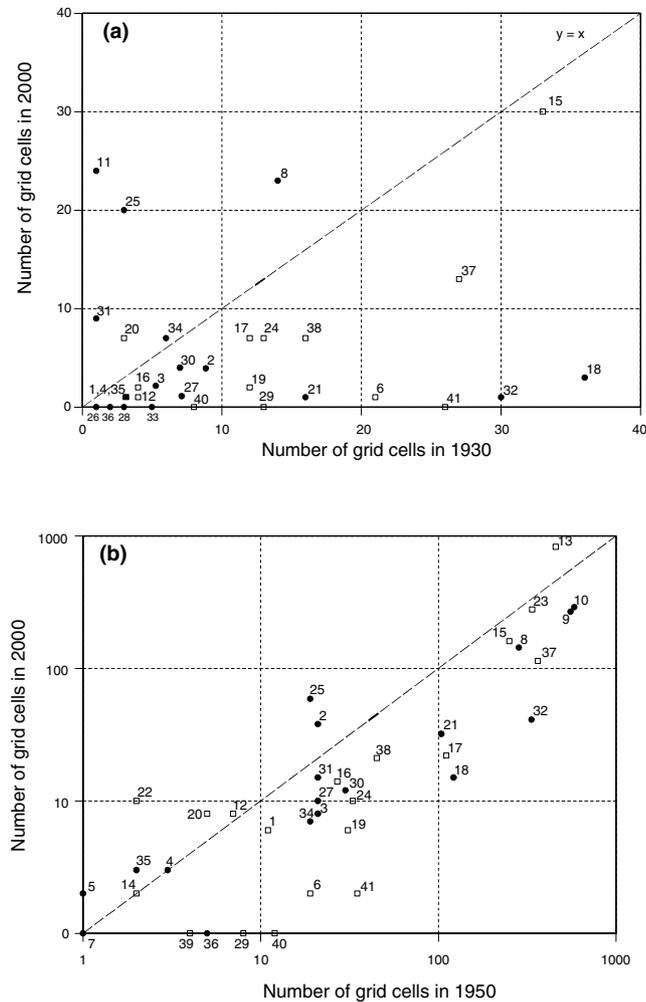


Fig. 1. Changes in distribution area for (a) 32 orchid species in Flanders and (b) 37 orchid species in the Netherlands. Points above the $y = x$ line (indicating no difference in distribution area between the two surveys) represent orchid species with an increased distribution range; points under this axis represent species of which the distribution area decreased between two survey periods (open squares: nectariferous orchids, full circles: nectarless species). 1, *Aceras anthroporum*; 2, *Anacamptis pyramidalis*; 3, *Cephalanthera damasonium*; 4, *C. longifolia*; 5, *C. rubra*; 6, *Coeloglossum viride*; 7, *Corallorrhiza trifida*; 8, *Dactylorhiza incarnata*; 9, *D. maculata*; 10, *D. majalis*; 11, *D. praetermissa*; 12, *Epipactis atrorubens*; 13, *E. helleborine*; 14, *E. muelleri*; 15, *E. palustris*; 16, *Goodyera repens*; 17, *Gymnadenia conopsea*; 18, *Hammarbya paludosa*; 19, *Herminium monorchis*; 20, *Himantoglossum hircinum*; 21, *Liparis loeselii*; 22, *Listera cordata*; 23, *L. ovata*; 24, *Neottia nidus-avis*; 25, *Ophrys apifera*; 26, *Ophrys fuciflora*; 27, *Ophrys insectifera*; 28, *Ophrys sphegodes*; 29, *Orchis coriophora*; 30, *Orchis mascula*; 31, *Orchis militaris*; 32, *Orchis morio*; 33, *Orchis palustris*; 34, *Orchis purpurea*; 35, *Orchis simia*; 36, *Orchis ustulata*; 37, *Platanthera bifolia*; 38, *Platanthera chlorantha*; 39, *Pseudorchis albida*; 40, *Spiranthes aestivalis*; 41, *Spiranthes spiralis*.

3.3. Nectar reward, orchid decline and regional extinction

The mean number of grid cells occupied by a species declined from 8.4 to 5.6 (33%) for non-rewarding species and from 13.9 to 5.6 (60%) for rewarding species in Flanders and from 119 to 52 (56%) and from 93 to 79

(15%) in the Netherlands. For both regions, there was, however, no relation between the percentage change in distribution area and nectar production (Mann–Whitney $Z = -0.04$, $P = 0.97$, Mann–Whitney $Z = -0.41$, $P = 0.68$, respectively). Eight of the 32 studied species (25%) went extinct in Flanders, five of which were nectarless orchids: *Orchis ustulata*, *Ophrys fuciflora*, *Ophrys sphegodes*, *Orchis palustris* and *Orchis simia*. Nectariferous species that went extinct were *Spiranthes aestivalis*, *S. spiralis* and *Orchis coriophora*. In the Netherlands, five of the 37 studied species (14%) went extinct, two of which were nectarless (*Corallorrhiza trifida* and *Orchis ustulata*) and three were nectariferous species (*Orchis coriophora*, *Pseudorchis albida* and *S. aestivalis*). Results of the logistic regression analyses showed that the probability of a species going extinct in Flanders was not related to nectar reward neither to initial distribution (model $\chi^2 = 0.17$, $P = 0.25$ and model $\chi^2 = 1.35$, $P = 0.25$, respectively). In contrast, regional extinction probability was related to initial distribution range in the Netherlands (model $\chi^2 = 8.65$, $P = 0.003$), but not to nectar reward (model $\chi^2 = 0.17$, $P = 0.67$).

3.4. Orchid decline and habitat preference

For both regions, orchid decline was significantly related to the habitats orchid species occurred in (Kruskal–Wallis $\chi^2 = 10.62$, $P = 0.014$ and $\chi^2 = 14.03$, $P = 0.003$ for Flanders and the Netherlands, respectively). Orchid species typically confined to wet grasslands and heathlands suffered greater losses than species that find their optimal growth conditions in calcareous grasslands or forests (Fig. 2(a) and (b)). Especially, orchids typically occurring in heathlands and nutrient-poor grass heaths (e.g. *Coeloglossum viride*, *Orchis morio*, *Pseudorchis albida*, *Spiranthes aestivalis* and *S. spiralis*) showed dramatic decreases (90% in Flanders and 69% in the Netherlands) in distribution area.

4. Discussion

Most orchid species showed a strong decrease in their distribution area. Similar declines in distribution range of orchid species as the ones demonstrated in this study have been reported by Leten (1989) for the French speaking part of Belgium (Wallonia). Using a similar approach, Hutchings (1987) documented changes in distribution area of the early spider orchid (*Ophrys sphegodes*). The species declined from fifty-three 10×10 km grid squares prior to 1930 to only 10 grid squares in 1987. *Orchis ustulata*, extinct in both Flanders and the Netherlands, decreased from 265 to 55 (80% decline) grid cells during the last 50 years in Britain (Tali et al., 2004). However, not all species showed a significant

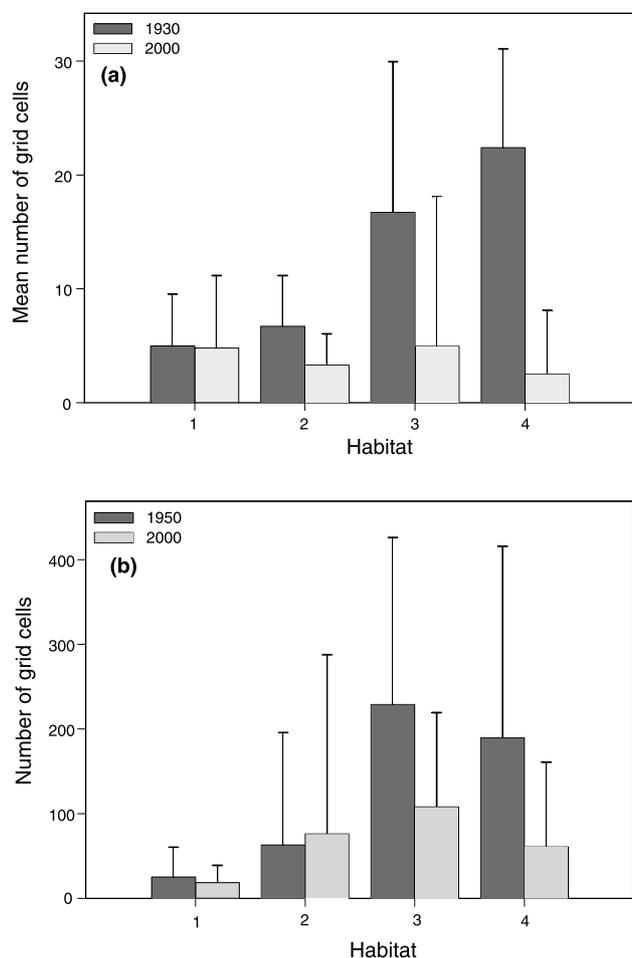


Fig. 2. Declines in distribution area of orchid species according to the habitats they occur in for (a) Flanders and (b) the Netherlands. 1, calcareous grasslands; 2, forests and forest edges; 3, wet grasslands and fens; 4, heathlands and nutrient-poor grass heaths.

decline in their distribution area and some of them were even able to expand their distribution range. Carey (1999) and Carey et al. (2002) found strikingly similar expansion rates for *Himantoglossum hircinum* in Great Britain, which the authors believed to be associated to changes in climatic conditions related to global warming. Thus, it appears that the reported values of decline or increase of orchid species are independent of the region studied. Indeed, the correlation coefficient between percentages change per species for Flanders and the Netherlands was significantly larger than zero ($r_s = 0.59$, $P < 0.001$, $n = 28$).

Darwin (1862) suggested that low levels of fruit set, which are characteristic for non-rewarding species (Dafni and Ivri, 1979; Gill, 1989; Neiland and Wilcock, 1998), might be associated with orchid rarity. Based on an analysis of the distribution of 51 orchid species in the UK, Neiland and Wilcock (1998) presented data that supported this hypothesis. It appeared that most rare species did not produce any nectar (10 out of 11 species

were nectarless). The results of this study, however, showed no such association: both for the Netherlands and Flanders, non-rewarding and rewarding species had similar distribution areas. Moreover, we were also not able to demonstrate associations between changes in distribution area and nectar production, nor between extinction probability and nectar reward. Thus, despite the myriad of processes that might affect the long-term persistence of plant species, nectar provision did not appear to be one of them.

Only a few studies have taken into account demographic data to study the importance of fruit set on population viability of orchid species (e.g. Calvo and Horvitz, 1990; Calvo, 1993). These studies have shown that an increased fruit production not necessarily translates into high population growth rates or higher long-term viability because other factors than seed set (e.g. a lack of recruitment) were probably more important in determining lifetime fitness. Therefore, they concluded that the importance of seed set on lifetime fitness might be limited for orchid species (Calvo and Horvitz, 1990; Calvo, 1993). Similar results have been obtained for *Gentiana pneumonanthe* (Oostermeijer, 2000). Reducing seed output by more than 50% hardly affected population viability of the species. However, Ackerman et al. (1996) demonstrated that when fruit and seed production of the deceptive orchid *Tolumnia variegata* were experimentally increased, also seedling recruitment and population growth rates increased. Thus, if nectar-producing orchids are favoured by large fruit production, one might expect higher recruitment rates and as a result lower extinction risks in the future. Our results did not show this. Likewise, the alternative hypothesis that nectariferous orchids were more susceptible to fragmentation processes due to Allee effects, was also not confirmed.

The results between nectar reward and orchid decline may have been obscured by a relationship between nectar reward and habitat preference. However, such a relationship was not observed ($\chi^2 = 3.99$, $P = 0.26$) and hence, orchid decline seems to be primarily driven by deterministic threats associated with the habitat types orchid species occur in. Especially, orchids typically occurring in nutrient poor grasslands and heathlands suffered the greatest losses. Habitat loss and deterioration due to nutrient enrichment and a lack of adequate management probably are the main factors causing these species to quickly disappear. Fertilization for example, has been shown to strongly decrease the number of flowering plants of *Orchis morio* (Silvertown et al., 1994), a species that suffered strong decreases in distribution area both in Flanders and the Netherlands. In addition, Jersáková et al. (2002) found that this species responded rapidly and in a negative way to a lack of management, but also very slowly to restoration of traditional management practises.

5. Concluding remarks

The primary aim of this study was to test Darwin's suggestion that orchid rarity was related to nectar reward. Further, we wanted to test the hypothesis that, if overall seed set was affected by fragmentation processes more strongly in nectariferous than in nectarless orchids, the former should be more susceptible to local extinction than the latter. Our results demonstrate that nectar reward may be of minor importance in determining long-term persistence of orchid species in present-day, highly fragmented landscapes. In their review of the influence of plant breeding system and pollination specialization on the reproductive response of plants to habitat fragmentation, Aizen et al. (2002) also found no evidence for the hypothesis that pollination specialization was related to susceptibility to fragmentation. Habitat loss and deterministic threats associated with habitat deterioration (changing nutrient conditions and increased competition, changes in water conditions and increased edge effects) are probably more important in determining population viability and extinction rates of orchid species. These results indicate that, irrespective of pollination mode or nectar reward, the long-term survival of orchid species cannot be guaranteed unless these threats are reversed. However, apart from deterministic threats imposed by habitat fragmentation and degradation, life history traits other than nectar reward may be important in determining persistence of orchid species. Fischer and Stöcklin (1997), investigating local extinctions in calcareous grasslands in the period 1950–1985, found that species with a short life cycle were more prone to local extinction compared to long-lived perennials. Similarly, Eriksson and Ehrlén (2001) found that species with a long lifespan and clonal growth form were more persistent to habitat deterioration and fragmentation than short-living species. Although the exact lifespan of many orchid species is still not known, our results suggest that especially short-living species [e.g. *Ophrys sphegodes* (half-life: 2 years (Hutchings, 1987)), *Coeloglossum viride* (half-life: 1.0–2.4 years (Willems and Melsers, 1998)) and *Orchis ustulata* (half-life: 0.9–3.2 years (Tali, 2002))] are most vulnerable to extinction. More data on orchid longevity and responses to fragmentation are, however, needed to determine the relative importance of seed set and orchid longevity on long-term population persistence.

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