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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.

Keywords: Extinction risk; Nectar reward; Orchid species; Population viability; Seed production

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 km^2 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 km^2 grid and in the Netherlands between 1950 and 2000 using a 5×5 km^2 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%