

WHEN IS AN ASYMMETRIC PLANT-POLLINATOR RELATIONSHIP SYMMETRICAL?

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ABSTRACT

The Orchidaceae is a highly evolved, pollinator orientated family with some of the most specialized pollination systems. It has been suggested that plant specialization should be considered along with the degree of specialization of the mutualist partners and that both sides of the mutualistic interaction need to be evaluated to gain insights into the response of species to habitat fragmentation. Here we raise the question of reward systems, in particular, species that are pollinated through deception. The model is applied to two specialist plant genera with different means of deception, food and sexual, and compare the levels of decline of the two genera throughout Europe. We show that there is a highly significant difference between *Dactylorhiza* (food deceptive) and *Ophrys* (sexually deceptive) in the rate of decline, with *Ophrys* suffering much stronger decline consistently across Europe.

Keywords: *Dactylorhiza*, deception, habitat fragmentation, *Ophrys*, Orchidaceae

Introduction

Intuitively, one would expect that habitat fragmentation would have a greater effect on the reproductive success of pollination specialist plants than generalist due to changes in pollinator communities. However, studies have suggested that this may not be the case, with no difference being recorded between the reproductive success of generalist and specialist plant species (Aizen et al. 2002; Vázquez and Simberloff 2002). Ashworth et al. (2004) suggested that plant specialization needs to be considered along with the degree of specialization of the mutualist partners and that both sides of the mutualistic interaction need to be evaluated.

There is a trend in the Orchidaceae towards a reduction in the number of pollinator species per orchid species resulting in increased specialization (Tremblay 1992). Orchid-pollinator interactions are often considered to be asymmetrical, with the orchid relying far more on its pollinator than the pollinator on the orchid. As Nilsson (1992) stated “interaction between two such unequally interdependent organisms inevitably results in the first being pushed around genetically by the second: pollinator traits govern any floral evolutionary trend.” An example of the asymmetrical orchid-pollinator relationship is the hawkmoth (*Panogena lingens*), which was found to pollinate at least 5 species of long-spurred angraecoid orchids (Nilsson et al. 1987). Such behaviour has also recently been recorded in other species of angraecoid orchids (Martins and Johnson 2007). In these cases the pollinator may only have adapted to access the nectar resource of long spurred orchids (Nilsson 1988). However, approximately one-third of orchids

have evolved mechanisms of deceit, where the pollinator receives no reward (van der Pijl and Dodson 1966; Ackerman 1984). In this situation, since there is no reward, the pollinator receives no benefits.

Ashworth et al. (2004) considered mutualistic plant-pollinator interactions. However, in the case of species that utilize deception as pollination strategy the relationship cannot be considered mutualistic. Rather the relationship may be considered parasitic since the pollinator does not receive a reward and therefore the relationship on the side of the pollinator may be neutral or even negative (Wong and Schiestl 2002).

Under asymmetric conditions the model (Ashworth et al. 2004) suggests that a generalist plant may have many different specialist and generalist pollinators whereas a specialist is likely to have few pollinators but those are expected to be generalists. The latter would seem to fit situations seen in orchid-pollinator interactions, particularly in the case of deceptive orchids, since how could a specialist pollinator (i.e. those that rely on one or a few plant taxa) be attracted and evolve to a deceptive orchid when there is no fitness benefit? This is seen in the food deceptive genus *Dactylorhiza* that relies often on bees to facilitate pollination while the bees visit numerous rewarding species (van der Cingel 1995).

However, in species that utilize sexual deception (pseudocopulation), such as *Ophrys*, the relationship is actually symmetrical with both sides being specialists. The orchid relies on one or few insect pollinators that visit the orchid for perceived sexual benefit (i.e. reproduction). The pollinator, therefore, is in fact a specialist since it is only interested in sexual liaisons with females of the same species; that is not to say that its foraging behaviour is not generalist.

Table 1 Rates of decline for *Dactylorhiza* and *Ophrys* species in 9 European countries of parts thereof.

	Country	UK	Ireland	Czech Rep.	Switzerland	Austria	Germany	Germany – Thuringen	Italy – Trentino	Estonia
t-test		0.14	0.15	0.36	0.12	0.02	0.62	0.85	0.28	–
	<i>Ophrys apifera</i> Huds.		49	25	66	53	22	45	53	
	<i>Ophrys bertolonii</i> formis O. Danesch & E. Danesch									
	<i>Ophrys holoserica</i> (Burm.f.) Greuter	33		44	59	94	53	100	29	
	<i>Ophrys holoserica</i> ssp. <i>holubiana</i> (András.) Dostál			100						
	<i>Ophrys insectifera</i> L.	59		100	52	48	19	34	25	13
	<i>Ophrys pseudobertolonii</i> Murr				50					
	<i>Ophrys sphegodes</i> Mill.	71	48		46	89	61	65	19	
	<i>Ophrys sphegodes</i> ssp. <i>araneola</i> (Rchb.) M. Lainz				65		80			
Average		54.3	48.5	67.3	56.3	71.0	38.8	64.8	31.8	13.0
	<i>Dactylorhiza baltica</i> (Klinge) N.I. Orlova									10
	<i>Dactylorhiza cruenta</i> (O. F. Müll.) Soó				28				0	17
	<i>Dactylorhiza fistulosa</i> H. Baumann & Künkele								56	
	<i>Dactylorhiza fuchsii</i> (Druce) Soó,	13	12	45				37	2	0
	<i>Dactylorhiza fuchsii</i> var. <i>sooana</i> (Borsos) Kreutz			0						
	<i>Dactylorhiza incarnata</i> (L.) Soó	44	39	56	60	38	34	80	36	14
	<i>Dactylorhiza lapponica</i> (Laest. ex Hartm.) Soó								0	
	<i>Dactylorhiza latifolia</i> (L.) Soó								19	
	<i>Dactylorhiza maculata</i> (L.) Soó	22	23	67	27		4			34
	<i>Dactylorhiza majalis</i> (Rchb.) P. F. Hunt & Summerh.	62	18	37	29	16	4	40		
	<i>Dactylorhiza ochroleuca</i> (Wüstnei ex Boll) Holub				66					
	<i>Dactylorhiza praetermissa</i> (Druce) Soó	20		66						0
	<i>Dactylorhiza purpurella</i> (T. Stephenson & T. A. Stephenson) Soó	21	46							
	<i>Dactylorhiza russowii</i> (Klinge) Holub									19
	<i>Dactylorhiza ruthae</i> (M. Schulze) Soó									0
	<i>Dactylorhiza sambucina</i> (L.) Soó				39	52	76	88		0
	<i>Dactylorhiza traunsteineri</i> (Saut. ex Rchb.) Soó	30	68		59	50	32		31	
Average		30.3	34.3	45.2	44.0	23.1	30.0	61.3	20.6	10.4
Historic sites (H)		pre 1986	pre 1986	pre 1980	pre 1977	pre 1956	pre 1945	pre 1990	pre 1970	pre 1970
Extant sites (E)		1987–1999	1987–1999	post 1980	post 1977	post 1957	post 1945	post 1990	post 1970	post 1970
References		Preston et al. 2002	Preston et al. 2002	Jatlová & Šmiták 1996	Reinhard et al. 1991	Polatschek 2001	Haeupler & Schonfelder 1989	Eccarius 1997	Perazza 1992	Kull & Tuulik 2002

If the model of Ashworth et al. (2004) holds, then we would expect sexually deceptive species to be more susceptible to habitat fragmentation than food deceptive species. Here we compare the decline of the food deceptive genus, *Dactylorhiza*, with that of the sexual deceptive genus, *Ophrys*, throughout Europe.

As an alternative hypothesis, one could expect that the rate of decline of sites of different orchid species within a genus would be negatively correlated with the number their pollinator species.

Methods

We used available data from regional flora atlases on the numbers of historic vs. extant sites from nine European countries or parts thereof, containing information on at least one species of *Dactylorhiza* and *Ophrys*. For each country, the rate of decline was calculated as the ratio of historic sites (H in Table 1) to that of all sites ever recorded (E + H in Table 1). We then compared the rate of decline in these two genera, using a two-factor ANOVA and a series of two-sample two-tailed t-tests assuming unequal variances. We correlated, using Pearson's correlation coefficient, the numbers of pollinator species with the rates of decline of sites for different *Ophrys* species. Only countries or regions with at least 4 *Ophrys* species were considered (Switzerland, Austria, Thüringen and Italy) using pollinator data from van der Cingel (1995).

Results

Table 2 shows that there is a highly significant difference between *Dactylorhiza* and *Ophrys* in the rate of decline, with the latter genus suffering much stronger decline. The t-tests (Table 1), however, show that when individual countries are considered, this difference is statistically significant only for Austria. Further, if Bonferroni correction is applied this result becomes not significant ($p = 0.17$). This means that it is the consistently stronger decline of *Ophrys* across Europe that is responsible for the significant difference (Fig. 1).

Table 2 Two-factor ANOVA without replication with factors Genus and Country and rate of decline as the response variable.

Source of Variation	SS	df	MS	F	P-value	F crit
Genus	1148	1	1148	13.94	0.006	5.32
Country	3941	8	493	5.98	0.010	3.44
Error	659	8	82			
Total	5749	17				

Correlation coefficients between the numbers of pollinator species and the rates of decline of sites for different

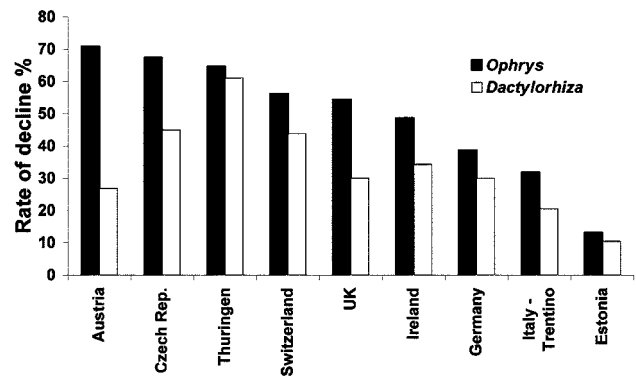


Fig. 1 Average rate of decline for two genera of terrestrial orchids, *Dactylorhiza* and *Ophrys*, in 9 European countries or parts thereof.

Ophrys species were all positive and not significant ($p > 0.05$) – $r = 0.72$ for Switzerland, $r = 0.26$ for Austria, $r = 0.49$ for Thüringen and $r = 0.64$ for Italy.

Discussion

These results indicate that species that utilize sexual deception are more prone to extinction than food deceptive species, that is to say specialist plants with symmetrical interactions are more sensitive than those with asymmetric interactions. Ashworth et al. (2004) are therefore correct in stating that “plant specialization cannot be considered in isolation from the degree of specialization of the mutualist partners” and that “evaluation of both sides of the mutualistic interaction will yield insights into the mechanisms behind species’ responses to habitat fragmentation”. However, the reward is the tangible benefit pollinators receive, although they are usually attracted to the flower in the first place through advertisement (Proctor et al. 1996). Therefore, the plant-pollinator relationships cannot be considered in isolation from the reward system even if the reward is from an unrelated source, such as in the case of sexual deception.

The outcome above is not affected by the length of the time periods from the countries studied, as this only affects the magnitude of the differences between results for the two genera, not the consistently larger decline in *Ophrys*. The longer the periods considered, the larger the difference.

The alternative hypothesis was not supported by our data. The number of pollinator species per orchid species did not significantly affect the rate of decline of orchid sites within the genus *Ophrys*. This again leaves us with the hypothesis of Ashworth et al. (2004) as the only plausible option. It should be noted that, while the underlying assumption of the paper is that reward system is the main difference between the genera, other possible generic differences such as in demography, fruit set, mycorrhizal specificity, clonality, etc. could contribute towards the different levels of decline seen. No evidence is

available to suggest this. Further, most differences such as in fruiting success, seed production, breeding system are indirectly, if not directly, related to the reward system (Cozzolino and Widmer 2005; Tremblay et al. 2005; Jersáková et al. 2006).

Conclusions

Ecosystem decay has led to a “pollination crisis” caused by the disruption in pollination systems. The cause of the crisis, human activity, is widespread and it is therefore likely that pollination disruption is also widespread (Buchmann and Nabham 1996). Not surprisingly then that there is a consistently stronger decline of *Ophrys* across Europe. However, when individual countries are considered, this difference is statistically significant only for Austria, although this becomes non-significant when Bonferroni correction is applied, suggesting that the cause is widespread, consistent and crosses international boundaries. Two such causes may be climate change or intensification of agriculture.

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