Consumptive emasculation: the ecological and evolutionary consequences of pollen theft

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ABSTRACT

Many of the diverse animals that consume floral rewards act as efficient pollinators; however, others 'steal' rewards without 'paying' for them by pollinating. In contrast to the extensive studies of the ecological and evolutionary consequences of nectar theft, pollen theft and its implications remain largely neglected, even though it affects plant reproduction more directly. Here we review existing studies of pollen theft and find that: (1) most pollen thieves pollinate other plant species, suggesting that theft generally arises from a mismatch between the flower and thief that precludes pollen deposition, (2) bees are the most commonly documented pollen thieves, and (3) the floral traits that typically facilitate pollen theft involve either spatial or temporal separation of sex function within flowers (herkogamy and dichogamy, respectively). Given that herkogamy and dichogamy occur commonly and that bees are globally the most important floral visitors, pollen theft is likely a greatly under-appreciated component of floral ecology and influence on floral evolution. We identify the mechanisms by which pollen theft can affect plant fitness, and review the evidence for theft-induced ecological effects, including pollen limitation. We then explore the consequences of pollen theft for the evolution of floral traits and sexual systems, and conclude by identifying key directions for future research.

Key words: pollen limitation, pollen parasitism, pollen robbery, pollination efficiency, cheating, toxic pollen, sexual systems.

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I. INTRODUCTION

Mating by angiosperms with granular pollen is highly inefficient, as typically <1% of the pollen removed from flowers reaches conspecific stigmas (Harder & Johnson, 2008). This low pollination efficiency has diverse ecological and evolutionary consequences. Poor success during pollen transport likely contributes significantly to the common pollen limitation of seed production in plant populations (Ashman et al., 2004). Low pollination efficiency also creates considerable opportunity for evolutionary improvement of pollination and mating systems via selection on floral traits (Harder & Routley, 2006). Indeed, angiosperm diversity correlates geographically with the incidence of pollen limitation in plant communities (Vamosi et al., 2006).

Consumption of pollen by animals may contribute significantly to the transport losses that are important causes of low pollination efficiency (Harder & Routley, 2006). Pollen provides an accessible, rich source of protein, which is consumed by a variety of invertebrates and vertebrates (Roulston & Cane, 2000; Roulston, Cane & Buchmann, 2000; Diaz & Kitzberger, 2006). These animals either consume pollen directly (e.g. Trigona bees, beetles, bats, syrphid flies, thrips), or collect it to feed their larvae (e.g. bees and masarid wasps). Because pollen provides the sole protein source for many of these animals, especially bees, it represents an essential resource for their existence and abundance, and is a key commodity in plant-animal interactions.

Pollen consumption necessarily reduces reproductive potential for both the affected plant's siring opportunities and, because of the reduced pool of pollen available for dispersal to stigmas, the plant population as a whole. Whether pollen consumption actually reduces pollination depends on the fate of other pollen that animals remove from flowers. Many flower visitors that consume pollen also transport it to stigmas and act as pollinators (Simpson & Neff, 1981; Buchmann, 1983), in which case the eaten pollen represents payment for services rendered. By contrast, other pollen consumers may effect no, or limited, pollination compared to that provided by a plant's efficient pollinators, so they act as pollen thieves that can directly reduce reproductive performance in the host-plant population (e.g. do Carmo, Franceschinelli & da Silveira, 2004; Diaz & Kitzberger, 2006). For example, introduction of honey bees (Apis mellifera L.) into foreign environments often disrupts pollination of native plants and can threaten their long-term viability (Paton, 1993; Vaughton, 1996; Gross & Mackay, 1998; Goulson, 2003; do Carmo et al., 2004).

Despite the potentially significant consequences of pollen theft for plant reproduction, and growing interest in the closely related topics of nectar theft (Irwin, Brody & Waser, 2001), pollen limitation (Ashman et al., 2004), cheating on mutualisms (Bronstein, 2001) and the effects of introduced species on native pollination systems (Traveset & Richardson, 2006), the occurrence and consequences of pollen theft have yet to receive much attention. Indeed, a search of the ISI Web of Science for ("nectar rob*" or "nectar theft" or "nectar thie*") in papers published from 1970 until July 2008 identified 154 citations, whereas a search with 'nectar' replaced by 'pollen' found 15 papers, of which only 10 addressed pollen theft from plants. Due to the potential importance of pollen theft in floral ecology and evolution, and its relevance as a conservation issue, a synthesis of the existing work that exposes gaps in current understanding and identifies relevant hypotheses is timely.

Herein we review available literature on pollen theft and consider its implications for plant reproduction. We first propose a comprehensive definition of pollen theft and apply it to published cases to identify animals that commonly act as thieves. We then summarize current understanding of the ecological and evolutionary effects of pollen theft and propose new hypotheses concerning these consequences. Finally, we discuss the evolutionary options for plants to escape pollen theft or mitigate its deleterious impacts on pollination.

(1) Who are pollen thieves?

All pollen thieves consume pollen directly and/or collect it to feed to their offspring; however, all thieves are not functionally equivalent from a plant's perspective. We define pollen foragers as thieves if they deposit so little of the pollen they remove onto conspecific stigmas that their absence from the prevailing assemblage of flower visitors would not reduce cross-pollination. If thieves damage flowers during theft we will refer to them as pollen robbers when the distinction is informative (by contrast, Inouye, 1980, included cases with no damage [theft] and damage [robbery] as classes of floral larceny). Within this definition, we recognize two classes of pollen thieves that differ in the consistency of their effects on the cross-pollination of a particular plant species: habitual thieves and conditional thieves.

Habitual thieves always remove pollen from a given plant species without depositing pollen on appropriate stigmas, and so universally reduce cross-pollination of the plant species involved. Habitual thieves include: animals that do not visit flowers when ovules are available for pollination, by avoiding female plants (e.g. do Carmo et al., 2004), female flowers, or dichogamous flowers in female phase (e.g. Paton, 1993); animals whose size, morphology and/or foraging behaviour while visiting receptive flowers

precludes stigma contact as they access pollen (e.g. Eguiarte & del Río, 1987; Weiss, 1996); and animals that do not carry pollen, such as slugs (e.g. Neijzing & Zeven, 1976). For example, unlike the resin-collecting bees that pollinate dioecious *Clusia arrudae*, introduced honey bees, which do not use resin, collect pollen from male trees while ignoring female trees (do Carmo *et al.*, 2004), and so never transfer pollen to stigmas.

Identification of conditional thieves is less straightforward, because they pollinate, but represent the minimum of the continuum in cross-pollination efficiency (e.g. Vaughton, 1996), delivering a trivial proportion of the pollen they remove from flowers to stigmas on other conspecific plants. This inefficiency by conditional thieves can arise for several reasons, including inappropriate flower manipulation to effect pollination reliably (e.g. Hurd & Linsley, 1963; Ish-Am & Eisikowitch, 1993) and/or a poor match between thief size and the positions of floral sex organs (e.g. Armbruster *et al.*, 1989). The essential feature of conditional thieves involves the presence of alternative efficient pollinators: they act as thieves if other visitors provide more efficient pollination, but serve as pollinators (albeit poor ones) when they are a plant's only visitors (Thomson & Thomson, 1992). Interestingly, an individual animal could act temporarily as a conditional thief while learning to manipulate flowers of a particular species (see Raine & Chittka, 2007), but as an efficient pollinator once it is experienced.

To identify animals that act as pollen thieves we searched for published studies that identified floral visitors as pollen thieves, pollen parasites or pollinivores (Inouye *et al.*, 1994) and/or documented pollen theft. The resulting 53 studies describe pollen theft (as defined here or by the authors) from more than 80 plant species in almost 40 families (Table 1). With one exception, all identified pollen thieves are invertebrates and, except for snails and mites, are flying insects that depend on pollen for protein. As a group, bees act most often as pollen thieves. The sole reported vertebrate pollen thief is a parakeet (*Enicognathus ferrugineus*) that selectively consumes pollen and male flowers of *Nothofagus pumilo*, a monoecious, wind-pollinated tree (Diaz & Kitzberger, 2006). Most documented cases of pollen theft involve species-level interactions, but individuals of an otherwise pollinating species may also act as thieves. For example, pollen- *versus* nectar-foraging honey bees often differ in their pollination efficiency: exclusive pollen foragers can act as thieves, whereas nectar foragers pollinate effectively (Ish-Am & Eisikowitch, 1993; Young, Dunning & von Hasseln, 2007).

Most identified pollen thieves (Table 1) effectively pollinate other plant species; thus pollen theft results not simply from intrinsic characteristics that predispose an animal to theft, but more generally from a mismatch between the ecologies and morphologies of the animal and plant involved. Nevertheless, some animals have been documented as pollen thieves much more frequently than others, such as the highly eusocial bees *Trigona* and *Apis* (Table 1). *Trigona* species are the only bees reported to chew through anthers to access pollen, and so may be less constrained by floral morphology that encourages stigma contact by pollen

collectors. Indeed, *Trigona* species that act as pollen thieves seem to do so habitually more often than conditionally. Honey bees (*Apis* spp.) also display remarkable flexibility in their manipulation of flowers, which could predispose them to pollen theft (Westerkamp, 1991). Given that bees are both the most important group of flower visitors worldwide (Danforth *et al.*, 2006), and the most frequently documented pollen thieves, pollen theft is probably much more widespread than indicated by the existing literature.

(2) Effects of pollen theft on plant reproduction

(a) Direct effects

Pollen functions directly in plant mating as the carrier of male gametes, so its removal by pollen thieves represents consumptive emasculation that can reduce siring opportunities directly (do Carmo *et al.*, 2004). Pollen theft can also cause pollen limitation at the population level by depleting the overall pool of male gametes available to fertilize ovules (Hargreaves, 2007). By contrast, nectar serves no direct role in plant reproduction, so its loss through theft can affect reproductive performance only indirectly.

Pollen theft directly degrades a plant's male and/or female fitness only if consumed pollen would otherwise have been deposited on stigmas. Three possible pollen fates arise during pollen removal: pollen remains in anthers after visits cease (removal failure); pollen is dislodged (e.g. by a "sloppy" flower visitor), but not carried away (removal loss); and visitors remove pollen, which then has a chance of being involved in self- or cross-pollination (Harder, 2000; Harder & Routley, 2006). If stolen pollen would otherwise have been involved in removal failure or loss, theft should not compromise plant fitness. Indeed, a negative relation between removal loss and potentially exportable pollen may underlie the evolution of pollination by pollen-collecting bees (Harder & Wilson, 1997). However, if theft consumes potentially exportable pollen, without a compensating reduction in removal loss, it reduces siring opportunities and, potentially, male fitness. Identification of the alternative fate(s) of stolen pollen will often be difficult, but theft directly from stigmas (Gross, 1993; Gross & Mackay, 1998) provides a rare exception, because this pollen was already deposited successfully and so is clearly stolen from the exported pollen pool. As thieves can probably remove only ungerminated grains, because germinated grains generally adhere firmly to stigmas (Ortega, Dicenta & Egea, 2007), direct theft from stigmas almost certainly reduces the siring success of the pollen donors, and can reduce female success directly as well (Gross & Mackay, 1998).

(b) Indirect effects

Pollen theft could also affect plant performance indirectly, much like nectar theft. Because pollen is not replaced after its removal, pollen theft cannot impose the energetic burden that can reduce fecundity after nectar theft (Inouye, 1980; Westerkamp, 1996). Rather, pollen (and nectar) theft may

Table 1. Documented occurrences of pollen theft as defined in the text or by the original authors, including the plants and animals involved and factors that contribute to theft. Studies were found by searching the ISI Web of Science (1972 to 2008) and CSA Biological Sciences (1960 to 2008) using the topic phrases "pollen theft*", "pollen thie*", "pollen rob*", "pollen parasit*", "pollinivor*" and "ugly pollinator*" and, to find studies in Spanish, "polen and (parasit* or rob*)". For each study of pollen theft, we then searched the literature that it cited and that cited it for additional accounts. Studies that documented theft by multiple visitor groups are listed in full under the main thief and again as additional references under other thieves.

Pollen thief	Plant species Family	Primary pollinators	Primary floral reward	Sexual system[a]	Reason animal acts as thief[b]	Thief habitual or conditional[c]	Reference
Hymenoptera, Apoidea (bees)							
Apis mellifera							
	Parkia clappertoniana Mimosaceae	bats	nectar	H (hk)	herkogamy	(H)	Baker & Harris (1957)
	Callistemon rugulosus Myrtaceae	birds (honey eaters)	nectar	H	herkogamy[d]	C	Paton (1993)
	Campomanesia pubescens Myrtaceae	large, buzz-pollinating bees	pollen	H (hk)	herkogamy[d] behaviour 1	H	Torezan-Silingardi & Del-Claro (1998)
	Salvia glutinosa Lamiaceae	Bombus spp.	nectar	H	herkogamy behaviour 1	(H)	Westerkamp (1991); Schremmer (1953)
	Amomum subulatum Zingiberaceae	Bombus spp.	nectar and pollen	H	herkogamy behaviour 1	H	Sinu & Shivanna (2007)
	Melastoma affine Melastomataceae	large buzz-pollinating bees	pollen	H (bz)	behaviour 1: collects pollen from stigma[d]	H	Gross & Mackay (1998)
	Impatiens capensis Balsaminaceae	Bombus spp.	nectar and pollen	H (♂♀)	behaviour 1[e] dichogamy[d]	C	Wilson & Thomson (1991)
	Correa reflexa Rutaceae	birds (honey eaters)	nectar	H	dichogamy[d]	C	Paton (1993)
	Persea americana Lauraceae	nectar-collecting honey bees	nectar	H (♀♂)	dichogamy	C: nectar foragers pollinate, pollen foragers do not	Ish-Am & Eisikowitch (1993)
	Grevillea barklyana Proteaceae	birds	nectar	H (♂♀)	dichogamy[d] reduced delayed selfing	C	Vaughton (1996)
	Clusia arrudae Clusiaceae	resin-collecting bee	resin	D	dioecy[d]	H	do Carmo et al. (2004)

also Baker et al. (1971)[d]; Moco & Pinheiro (1999)[d]; Eguiarte & del Río (1987)

Taxon / Plant species	Legitimate visitor	Reward		Mechanism	Code	Reference
Trigona spp.[f]						
Crescentia alata / Bigoniaceae	bats	nectar	H	herkogamy	(H)	del Río & Bullock (1990)
Dalechampia magnoliifolia / Euphorbiaceae	male euglossine bees	fragrance	M	herkogamy	C	Armbruster *et al.* (1989)
Aphelandra golfoduleensis / Acanthaceae; *Justica aurea* / Acanthaceae	hummingbirds	nectar	H (*A.g.*= hk)	herkogamy behaviour 1	(H)	McDade & Kinsman (1980)
34 unspecified spp.; *Melastoma affine* / Melastomataceae	large buzz-pollinating bees	pollen	H (bz)	herkogamy behaviour 2	H	Renner (1983); Gross (1993)
Cochlospermum vitifolium / Cochlospermaceae	*Xylocopa* and *Centris* bees	pollen	H (bz)	herkogamy or behaviour 1	(H)	Snow & Roubik (1987)
Theobroma cacao / Sterculiaceae	flies	nectar	H	behaviour 1	H	Young (1981; 1985)
Medicago sativa, *Astragalus sinicus* Fabaceae	bees	nectar?	H	behaviour 1	?	Tezuka & Maeta (1995)
Thunbergia grandiflora / Acanthaceae	bees	nectar	H	? chew off anthers[d]	?	Young (1983)
Bromelia antiacantha / Bromeliaceae	hummingbirds, maybe *Bombus* spp.	nectar	H	?	?	Canela & Sazima (2005)
also Moco & Pinheiro (1999); Raju & Rao (2006); Bullock *et al.* (1989)						
Halictidae						
Datura spp. / Solanaceae	hawkmoths	nectar	H	herkogamy	(H)	Thorp (2000)
Campanula americana / Campanulaceae	*Bombus*	pollen	H (♂♀)	dichogamy	(C)	Johnson *et al.* (1995); Lau & Galloway (2004)
Passiflora foetida / Passifloraceae	colletid bees	nectar	H	?	?	García & Hoc (1998)
also Baker *et al.* (1971); Moco & Pinheiro (1999); Renner (1983); Armbruster *et al.* (1989)						
Perdita spp.						
Mentzelia decapetala / Loasaceae	sphingid moths	nectar	H	herkogamy	H	Michener (1979)
Opuntia phaeacantha / Cactaceae	large bees	nectar?	H	herkogamy behaviour 1	H	Barrows *et al.* (1976)
Proboscidea arenaria / Martyniaceae	same as thief	nectar and pollen	H	behaviour 1	C	Hurd & Linsley (1963)
Bombus spp.						
Tolmiea menziesii / Saxifragaceae	fungus gnats	nectar	H (♂♀)	dichogamy small pollen loads	H	Goldblatt *et al.* (2004)
also Baker *et al.* (1971), Eguiarte & del Río (1987)						

Table 1. (cont.)

Pollen thief / Plant species Family	Primary pollinators	Primary floral reward	Sexual system[a]	Reason animal acts as thief[b]	Thief habitual or conditional[c]	Reference
mixed bees						
Swartzia apetala Fabaceae	buzz-pollinating solitary bees	pollen	H (bz)	herkogamy	(C)	Moco & Pinheiro (1999)
unspecified spp. Melastomataceae	large buzz-pollinating bees	pollen	H (bz)	herkogamy	depends on the species	Renner (1983)
Rhododendron calendulaceum Ericaceae	butterflies	nectar	H	herkogamy	(H)	Blair & Wolfe (2007)
Prockia crucis Flacourtiaceae	*Centris* and *Xylocopa* bees	pollen	H	herkogamy	(H)	Bullock *et al.* (1989)
Pseudobombax ellipticum	bats and birds (orioles)	nectar and pollen	H	herkogamy	(H)	Eguiarte & del Río (1987)
Ceiba acuminata / *Ceiba pentandra* Malvaceae	bats	nectar	H (hk)	herkogamy timing	H	Baker *et al.* (1971); Baker & Harris (1959)
Pongamia pinnata Fabaceae	larger bees	nectar and pollen	H (keel)	behaviour 2: too small to depress keel petals	C	Raju & Rao (2006)
8 spp. (6 genera) Malpighiaceae	oil-collecting bees	oil, rarely pollen	H (♀♂)	behaviour 2: rarely rupture stigmatic cuticle as needed to deposit pollen	C	Sigrist & Sazima (2004)
Heracleum sphondylium Apiaceae	some flies and beetles	nectar and pollen	H (♂♀)	dichogamy	(H)	Zych (2007)
Coleoptera (beetles)						
Isomeris arborea Capparaceae	likely *Bombus* spp.	nectar and pollen	A	larvae consume developing anthers	H	Krupnick & Weis (1999); Krupnick *et al.* (1999)
Zea mays Poaceae	wind	—	H	?	H	Lundgren *et al.* (2004)
Banksia menziesii Proteaceae	birds (honey eaters)	nectar	H (♂♀)	do not deposit enough pollen to pollinate	H	Ramsey (1988*a, b*)
Aconitum lycoctonum Ranunculaceae	long-tongued *Bombus* spp.	nectar	H (♂♀)	?	?	Utelli & Roy (2001)
Trevoa quinquenervia Rhamnaceae	flies, bees and beetles	nectar and pollen	A (♂♀)	?	(C)	Medan & D'Ambrogio (1998)

Group	Species / Family	Pollinator	Reward	Sexual system	Notes	Thief status	Reference
Diptera (flies)	*Plantago* sp. Plantaginaceae grasses Poaceae	wind	—	H	herkogamy? small pollen loads	?	Holloway (1976)
	Centropogon solanifolius[f] Campanulaceae	hummingbirds	nectar	H (dc)	larvae eat anthers in bud and leave before flower matures	H	Weiss (1996)
	Galeopsis speciosa Lamiaceae	long-tongued *Bombus* spp.	nectar and pollen	H	unlikely to carry pollen on proboscis	C	Schremmer (1953)
	Tolmiea menziesii Saxifragaceae	fungus gnat	nectar	H (♂♀)	dichogamy small pollen loads	H	Goldblatt *et al.* (2004)
	Heracleum sphondylium Apiaceae	some flies and beetles	nectar and pollen	H (♂♀)	dichogamy	(H)	Zych (2007)
Other mites and thrips	*Hamelia patens* Rubiaceae	hummingbirds	nectar	H	herkogamy	(H)	Paciorek *et al.* (1995)
	Actinidia deliciosa Actinidiaceae	bees	pollen	D	?	?	Kirk (1987)
	Echium plantagineum Boraginaceae	bees	nectar and pollen	H	eat pollen from stigmas	?	Kirk, Raju Rao (2006)
unknown insect[f]	*Gelsemium sempervirens* Loganiaceae	bees	nectar	H (ds)	never observed	?	Leege & Wolf (2002)
snails and slugs[f]	*Streptocarpus* sp. Gesneriaceae	insects	?	H	? presumably do not carry pollen	H	Neijzing & Zeven (1976)
Enicognathus ferrugineus (parakeet)[f]	*Nothofagus pumilio* Nothofagaceae	wind	—	M	preferentially consumes ♂ flowers, damages ♀ flowers instead of pollinating	H	Diaz & Kitzberger (2006)

[a] Sexual system: A = andromonoecious, D = dioecious, H = hermaphroditic, M = monoecious. Additional information about floral design is included in parentheses when provided by the original authors: bz=buzz-pollinated, dc=dichogamous (♂♀=protandrous, ♀♂=protogynous), ds=distylous, hk=herkogamous, keel=keel flower.

[b] The reasons that pollen thieves are designated as such include: behaviour [thief's pollen-collecting behaviour is inappropriate for pollinating, because it (1) enters or manipulates flowers in the 'wrong' position for stigma contact, or (2) is unable to trip a trigger required for pollination]; dichogamy (thief visits primarily/only male-phase flowers); dioecy (thief visits only male plants); herkogamy (thief is too small to contact stigma while collecting/consuming pollen); and timing (thief visits flowers after opportunities for pollination are over). C=conditional, (C)=probably conditional (some pollination likely but not measured), H=habitual, (H)=probably habitual (pollination by thief unlikely but not measured), ?=unknown.

[d] Thief is not native where pollen theft occurs.

[e] Pollen-collecting individuals only.

[f] Thief acts as a pollen robber; damaging the flower to access pollen.

influence plant fitness indirectly when it affects the behaviour of pollinators that visit later. Whereas nectar availability cannot usually be assessed before visitation (but see Goulson, Hawson & Stout, 1998; Raguso, 2004 for special exceptions), pollen often serves as a floral attractant and both nectar- and pollen-collecting pollinators use its absence to identify and avoid flowers that have been visited recently (Dobson & Bergstrom, 2000; Lunau, 2000). Damage to flowers by pollen robbers, which is particularly common for species with flowers that conceal pollen (Renner, 1983; Snow & Roubik, 1987; Gross, 1993), could aggravate this problem if it provides pollinators with additional deterring cues (Renner, 1983; Krupnick, Weis & Campbell, 1999). Regardless of the behavioural mechanism involved, reduced attractiveness to pollinators due to theft would cause pollinator limitation of pollen dispersal.

Unless flowers are damaged, pollen theft from plants that conceal pollen probably affects the behaviour of attracted pollinators in a manner similar to nectar theft, because pollen-collectors must visit flowers to assess pollen abundance. In the case of nectar theft, legitimate pollinators leave inflorescences that have experienced recent theft sooner than they would otherwise (reviewed in Maloof & Inouye, 2000). Pollen-collecting pollinators of plants with concealed pollen probably respond similarly to pollen theft, because they visit partially depleted flowers more rapidly and visit fewer flowers per inflorescence (Buchmann & Cane, 1989; Harder, 1990; Shelly & Villalobos, 2000). The latter response can diminish overall pollen import, but whether pollen export (i.e. successful dispersal) also suffers depends on how this reduction affects self-pollination between flowers (geitonogamy). Because geitonogamy directly reduces the amount of pollen on pollinators that is available for dispersal to other plants (Harder & Barrett, 1995), processes that divert removed pollen from geitonogamy can enhance export. Geitonogamy tends to increase with the number of flowers that each pollinator visits per inflorescence (Barrett, Harder & Cole, 1994; Karron et al., 2004; Harder & Johnson, 2005; Jersáková, Johnson & Kindlmann, 2006), so theft that promotes early visitor departure could reduce geitonogamy and enhance pollen export. However, the geitonogamy-reducing benefits of theft require subsequent pollinators to acquire significant pollen loads despite spending less time on an inflorescence, which seems unlikely if theft has already reduced pollen availability. Overall, the reproductive consequences of pollen theft will depend largely on whether any positive indirect effects of pollen consumption outweigh the negative direct and indirect effects.

II. ECOLOGICAL CONSEQUENCES OF POLLEN THEFT

Studies that consider pollen thieves as floral larcenists rarely measure the effects of theft on pollen export, pollen import or seed production, so information concerning the consequences of pollen theft for plant reproduction must be sought primarily in the literature on inefficient pollination

and florivory. Of the 53 studies that identified pollen theft (Table 1), only 12 considered its reproductive consequences (Table 2). The lack of studies that test conclusively (or even attempt to measure) the effects of pollen theft on plant performance is the greatest deficiency of the existing literature on floral larceny. Therefore, we also consider methods for quantifying the effects of pollen theft.

(1) Pollen limitation

Pollen limitation of seed production is a direct, and probably common, ecological effect of pollen theft for plants. Pollen limitation can result from either or both of two causes; quantity limitation occurs when pollinators disperse too few pollen grains to maximize seed set, whereas quality limitation occurs when the genetic quality of delivered pollen is sub-optimal, such that it fertilizes few ovules, or few fertilized embryos develop into seeds (Aizen & Harder, 2007). Although pollen limitation seems to occur commonly (Ashman et al., 2004; Knight et al., 2005), whether this represents chronic pollen limitation or stochastic fluctuations around long-term pollination averages remains to be determined for most cases (Thomson, 2001), as does the relative importance of quantity and quality limitation. Furthermore, the contribution of pollen theft to pollen limitation is largely unexplored.

As pollen thieves consume pollen, theft has considerable potential to cause quantity limitation of both siring success and seed production. Two experimental studies have demonstrated such effects. After observing that grasshoppers consumed many flowering plants of two highly protogynous grass species before they reached male phase, Bertness & Shumway (1992) excluded grasshoppers from grass stands, which increased the number of male-phase plants and produced a fivefold increase in seed set of undamaged ovules. In a study of a more typical situation, Hargreaves (2007) added honey-bee hives during half the flowering season to four populations of bird-pollinated Aloe maculata, which increased pollen removal by up to 50%, but reduced pollen receipt and seed set by up to 70% and 60%, respectively. Both of these studies demonstrate that pollen consumption can severely reduce seed production in plant populations.

The possible role of pollen theft in quality limitation of seed production is less obvious. Theft might cause quality limitation if thieves preferentially collect pollen of higher nutritional value (e.g. protein content or pollen-grain size; Robertson et al., 1999; Hanley et al., 2008) and nutritional quality is correlated with reproductive potential (Robertson et al., 1999; Roulston et al., 2000). Alternatively, theft could improve the genetic quality of pollen receipt indirectly if its effects on floral rewards for pollinators reduced geitonogamy (see Section I.2b), somewhat counteracting the impact of theft on quantity limitation.

(2) Measurement of the impact of pollen theft

The role of pollen theft in pollen limitation is difficult to demonstrate empirically. Given our definition of pollen

Table 2. Summary of studies that assessed the effects of pollen theft on plant fitness.

Plant species Family	Pollen thief	Conditional or habitual theft[1]	Consequence of pollen theft for plant reproduction Male	Female	Reference
Clusia arrudae Clusiaceae	honey bees[2]	H	pollen on anthers and pollinators reduced by ~99%	frequency of theft negatively correlated with seed set ($r = -0.9$)	do Carmo *et al.* (2004)
Melastoma affine Melastomataceae	honey bees[2]	H	thief collected pollen from stigmas; reduced siring success of donors whose pollen was removed	when last visitor was a thief, theft from stigma reduced fruit set by 10-28% and seed set by 53%	Gross & Mackay (1998)
Callistemon rugulosus Myrtaceae	honey bees[2]	C	apparent reduction in average siring success, given effects on female success	as bee visitation increased, fruit set decreased in open plants, but increased in absence of pollinators (caged plants)	Paton (1993)
Campomanesia pubescens Myrtaceae	honey bees[2]	C	thieves remove most pollen before pollinating bees are active	pollinator avoid plants being visited by thieves	Torezan-Silingardi & Del-Claro (1998)
Correa reflexa Rutaceae	honey bees[2]	C	simulation of theft by anther removal from donor flowers reduced pollen deposition on recipient flowers	as for male number of flowers receiving pollen also decreased	Paton (1993)
Grevillea barklyana Proteaceae	honey bees[2]	C	theft reduced seed set to 50% that of unvisited flowers by preventing delayed selfing	as for male when avian pollinators were common, theft did not result in pollen limitation	Vaughton (1996)
Campanula americana Campanulaceae	halictid bees	U	decreased siring success when pollinators rare, no effect when pollinators common	—	Lau & Galloway (2004)
Ceiba pentandra *Ceiba acuminata* Malvaceae	bees	H	none: theft occurs after pollination opportunity over	as for male	Baker & Harris (1959); Baker *et al.* (1971)
Pseudobombax ellipticum Malvaceae					Eguiarte & del Río (1987)
Isomeris arborea Capparaceae	beetle[3]	H	pollen export of undamaged flowers reduced by 50%, no decrease in selfing rate	reduced pollen receipt on damaged flowers, pollen limitation not detected	Krupnick & Weis (1999)
Centropogon solanifolius Campanulaceae	fly larvae	H	theft shortened or eliminated male phase	—	Weiss (1996)
Nothofagus pumilio Nothofagaceae	parakeet[3]	H	apparent reduction in average siring success, given effects on female success	theft reduced seed density sixfold compared to parrot-excluded branches	Diaz & Kitzberger (2006)

[1] H = habitual, C = conditional, U = unknown, see text for explanation of categories.
[2] Thief is not native where pollen theft occurs.
[3] Thief acts as a pollen robber, damaging flowers to access pollen.

theft, it could be assessed most directly by removing thieves from the environment and testing for an increase in pollination and seed set (e.g. Bertness & Shumway, 1992). However, removal of thieves without affecting pollinators is often impossible, so an alternative approach of increasing thief abundance and testing for reduced pollination and seed set may typically be more feasible (e.g. Hargreaves, 2007; also see Thomson, 2001).

If thief abundance cannot be manipulated, the effect of theft on female success could be assessed by relating temporal or spatial variation in average seed set to measures of both pollen dispersal (e.g. pollen loads on pollinators) and the intensity of theft. The only explicit study of pollen theft from a dioecious species provides perhaps the best example of the detrimental effects of pollen theft on seed set. Pollen-collecting honey bees visited only male plants of *Clusia arrudae*, clearly acting as pollen thieves (do Carmo *et al.*, 2004). Honey bees reduced the pollen loads of legitimate pollinators (resin-collecting bees) by >99%, and seed set of female plants varied negatively with honey-bee abundance (do Carmo *et al.*, 2004).

Pollen theft may affect the siring success of individual plants, even in the absence of pollen limitation in the population as a whole. Definitive demonstration that pollen theft reduces siring success requires tracking pollen from specific pollen donors, so that export can be correlated with the intensity of pollen theft for individual plants. Unfortunately, the most commonly used pollen-tracking techniques for studying pollen export (emasculation of recipient flowers and use of powder pollen analogues: Kearns & Inouye, 1993) are probably of limited use, because they could affect the attractiveness of flowers to pollen collectors. An alternative, indirect method would be to quantify pollen loads acquired by legitimate pollinators (e.g. do Carmo *et al.*, 2004), as reduced pollen loads in the presence of thieves (or simulated theft; Paton, 1993) suggest that some stolen pollen could otherwise have been picked up by pollinators and thus was available for export. Instead of tracking pollen, seed paternity could be assessed with genetic markers, such as allozymes or microsatellites (reviewed in Bernasconi, 2003). The only study of pollen theft to employ paternity analysis to date found that halictid pollen thieves reduced relative pollen export in experimental arrays only when pollinators were scarce (Lau & Galloway, 2004). Assessment of the effects of pollen theft with genetic markers requires careful experimental design to account for post-pollination processes, such as inbreeding depression, and fitness differences among donors. If these problems can be addressed, genetic paternity analysis could also be used to test the effects of floral traits that could ameliorate pollen theft (discussed further in Section III.1).

III. EVOLUTIONARY CONSEQUENCES OF POLLEN THEFT

As with reproduction in general, selection caused by pollen theft should often act asymmetrically with respect to the sex roles. Whenever it reduces pollen export, pollen theft will reduce siring opportunities and so affect phenotypic selection on reproductive traits that promote male function. By contrast, theft will influence selection on female traits only if it reduces pollen import sufficiently to cause pollen limitation. We now consider possible influences of pollen theft on the evolution of floral traits and sexual systems.

(1) Adaptation of floral traits

When pollen theft decreases plant reproduction differentially among phenotypes, selection should favour traits that reduce theft or its impact. As with plant responses to other antagonists, the possible evolutionary responses to pollen theft include tolerance through traits that mitigate the impact of theft, and resistance through traits that reduce the occurrence of theft either *via* plant or pollen defences against thieves or through escape in time or space. In addition, theft may be alleviated by a third evolutionary option not applicable in response to other antagonists, namely conversion, whereby pollen thieves are co-opted to become pollinators. These evolutionary responses are non-exclusive, and the type(s) that evolve will depend partially on whether thieves act habitually or conditionally; all options may be effective against conditional thieves, whereas habitual thieves probably cannot be converted to pollinators, but may be deterred successfully by anti-theft mechanisms. Although some of these characteristics could arise as correlated responses to interactions with other antagonists or pollinators, we discuss them here as potential responses to theft that could be selected directly.

(a) Tolerance

Many factors influence floral evolution, including pollinators, herbivores, and abiotic conditions (Strauss & Whittall, 2006), which may constrain the evolutionary ability of flowers either to escape or to resist pollen thieves, or to use them as pollinators. Nevertheless, chronic pollen loss to thieves could select for increased pollen production (more flowers or more pollen per flower) if it mitigated the effects of pollen theft, much as mast seeding is proposed to (over)compensate for losses to seed predators (Kelly & Sork, 2002). Unlike induced tolerance to herbivory through compensatory regrowth after attack, tolerance to pollen theft, if it occurs, is more likely preventative, because pollen loss to thieves should be indistinguishable from pollen removal by efficient pollinators. Pollen robbery may provide exceptions, because floral damage can stimulate increased flower production (McCall & Irwin, 2006; Wise, Cummins & De Young, 2008). However, whether such a response could be induced by minor damage, rather than loss of entire flowers or inflorescences, remains unknown.

Elevated pollen production will compensate for theft only if the intensity of theft does not increase proportionally through corresponding increases in thief abundance caused by elevated resource (pollen) availability (numerical response) and/or increased attraction of existing thieves from other, less-rewarding plant species (functional response) (Stanton *et al.*, 1991). Indeed, the best examples of predator satiation by mast seeding are large, dominant species whose seed abundance can control seed-predator populations, reducing their numbers during years of low seed production that separate high-production events (reviewed in Kelly & Sork, 2002). When mast seeding is associated with mast flowering (rather than greater fecundity per flower), plants may escape both pollen and seed predators. However, given

the more direct effect on plant reproduction, escape from seed predators likely affects the evolution of masting more strongly than escape from pollen thieves. In addition, compensatory pollen production may be subject to an evolutionary hurdle that is irrelevant to tolerance of herbivory, namely inbreeding. Because many pollen collectors forage longer on highly rewarding flowers or plants (see Section I.2*b*), increased pollen production could also increase within- and among-flower self-pollination. Elevated pollen production may therefore be effective only in combination with floral mechanisms that limit pollen removal by individual visitors (Harder & Thomson, 1989).

No studies have tested for compensatory pollen production while controlling for phylogeny, but the literature on pollination by pollen-collecting bees provides related evidence, because their activity should similarly select for increased pollen production (see Cruden, 2000). Buzz pollination, which usually involves pollen-rewarding flowers, is sometimes associated with unusually high pollen production per flower (Buchmann, 1983; L.D. Harder, unpublished data). However, a study of six buzz-pollinated Pyrolaceae species did not find consistently lower pollen production in the two species that also produce nectar (Knudsen & Olesen, 1993), as would be expected if elevated pollen production served to compensate its use as a reward.

(b) Resistance

As with anti-herbivory adaptations, plants can resist antagonists by escaping in time or space, or using chemical and/or physical deterrents. In general, anti-theft adaptations should evolve through selection on male function, as theft reduces individual siring opportunities directly, whereas it usually affects female function indirectly. However, pollen theft can affect female fitness directly in largely self-pollinating species and when it reduces the attractiveness of flowers to primary pollinators. Such cases could promote the evolution of anti-theft traits *via* selection on female fitness.

(*i*) *Escape in time.* Different foraging periods for pollen thieves and pollinators could select on the timing of pollen presentation. As most pollen thieves are diurnal insects (Table 1), flowers that open only nocturnally should be less susceptible to pollen theft. Indeed, bat-pollinated *Crescentia alata* trees whose flowers open later during the evening experienced less pollen theft by bees than trees whose flowers opened earlier (del Río & Bullock, 1990). Early-morning pollen collection from bat-pollinated species with short-lived flowers is inconsequential for reproduction, because all possible pollination occurs during the preceding night (Baker, Cruden & Baker, 1971; Gribel, Gibbs & Queiroz, 1999). Note that visitors that collect residual pollen after pollination is complete are scavengers, but not pollen thieves under our definition, even if they never contact stigmas. Early-morning anthesis could allow diurnal flowers to reduce pollen theft if pollinators begin foraging before pollen-collecting insects, as is common for nectarivorous birds (e.g. Ramsey, 1988*a*; Timewell & MacNally, 2004) and possibly some euglossine bees (Pan-

sarin, Bittrich & Amaral, 2006). However, prior access by pollinators is not beneficial when thieves steal pollen directly from stigmas, as stolen pollen will not be replaced by pollinators (Gross & Mackay, 1998).

(*ii*) *Escape in space: cryptic pollen.* Pollen can act as a visual or olfactory pollinator attractant (Dobson & Bergstrom, 2000; Lunau, 2000; Pernal & Currie, 2002), so pollen concealment could reduce theft. Visually cryptic or odourless pollen may reduce floral attractiveness to pollen collectors, limiting visitation by thieves. Hermaphroditic flowers of some species produce less-fertile, but more visible, decoy pollen to attract pollen-feeding pollinators, whereas their viable pollen is cryptic, presumably to reduce its consumption (Vogel, 1978; Hrycan & Davis, 2005). Similarly, Faden (1992) found that only the sterile pollen in the upper stamens of nectarless *Palisota hirsute* flowers produces scent, presumably to lure pollen consumers from the scentless fertile pollen. Cryptic pollen should be especially beneficial in species pollinated by nectarivores, for which pollen is less likely to serve as a signal. Bird-pollinated cacti produce brown-red pollen more often than their insect-pollinated relatives, which generally produce bright yellow pollen (Rose & Barthlott, 1994). Rose & Barthlott (1994) concluded that birds are less likely to groom cryptic, dark pollen from their bills, as has been proposed for bird-pollinated orchids with dark pollinia (Dressler, 1971; Inouye, 1975). However, cactus pollen accumulates primarily on facial feathers where birds cannot see it, so cryptic pollen may serve primarily to lessen detection by pollen thieves, as many pollen-collecting insects innately prefer highly contrasting and/or yellow pollen (Lunau, 2000).

(*iii*) *Escape in space: inaccessible pollen.* Consistent differences between pollinators and pollen thieves in size, strength, or ability may select for physical concealment of pollen and/or trigger mechanisms that must be tripped to expose it. Ramsey (1988*a*, *b*) suggested that the explosive opening of *Banksia menziensii* flowers, which can be triggered only by birds, evolved to limit pollen loss to pollen-thieving staphylinid beetles. Flowers of some species, such as those in the Lecythidaceae (Mori, Orchard & Prance, 1980), Fabaceae (Yeo, 1993; Westerkamp, 1997), and Polygalaceae (Westerkamp, 1999), have hood-like petals or other protective structures that must be pushed aside to access rewards, preventing access by smaller visitors. Buzz pollination, which requires vibration of poricidal anthers to release pollen, typically occurs in bee-pollinated plants that provide only pollen as a pollinator reward (Buchmann, 1983) and enables plant species to restrict pollen access to legitimate pollinators (Harder & Barclay, 1994). Nevertheless, some buzz-pollinated species suffer pollen theft from small bees that can buzz only individual anthers and so do not contact stigmas (Renner, 1983), *Trigona* bees that chew poricidal anthers to access pollen (Renner, 1983; Snow & Roubik, 1987; Gross, 1993), or theft of unprotected pollen on stigmas (Gross & Mackay, 1998).

(*iv*) *Deterrents: pollen structure.* Pollen that is unattractive or detrimental to pollen thieves could eliminate pollen theft altogether, especially for plants not pollinated by

pollen consumers. For example, pollen may be rendered inedible by packaging into pollinia, as in most orchids (Orchidaceae; Johnson & Edwards, 2000) and milkweeds (Asclepiadaceae; Verhoeven & Venter, 2001). Many of the most common pollen consumers, including bees, do not collect or consume pollinia (Thorp, 2000). Certain pollen feeders may also be deterred by the structure of individual grains, such as the long spines on pollen grains of cotton (*Gossypium hirsutum*) and okra (*Abelmoschus esculentus*; Vaissière & Vinson 1994).

(*v*) *Deterrents: chemical defence.* Chemical defences in leaves and bark are well known for their ability to deter herbivores, and similar chemicals can exist in floral tissues (McCall & Irwin, 2006). Floral 'toxins' have been suggested as a deterrent against corolla-piercing nectar robbers (Inouye, 1983 and references therein) and may also defend against corolla- or anther-piercing pollen robbers, such as *Trigona* bees. Alternatively, sticky, glandular corollas can dissuade potential nectar robbers from landing to access nectar through pierced corollas (Schremmer, 1953), and could presumably deter pollen robbers from piercing corollas as well.

In addition to well-documented chemicals in floral and leaf tissues, pollen itself can contain diverse secondary compounds, including many that are repellent or toxic to certain animals (Detzel & Wink, 1993; Roulston & Cane, 2000; Pimentel de Carvalho & Message, 2004; Cintra *et al.*, 2005). As with repellent nectar and floral toxins, repellent or toxic pollen may simply be a pleiotropic consequence of chemical defence against herbivores in other tissues (Adler, 2000), but it may also serve to filter floral visitors (Johnson, Hargreaves & Brown, 2006). For example, some volatile compounds in the pollen odours of wind-pollinated plants likely evolved to deter pollen thieves (Dobson & Bergstrom, 2000). The effectiveness of deterrence depends on the ability of pollen thieves to recognize noxious pollen. Several laboratory studies have shown that honey bees can distinguish between concentrations of secondary compounds in either pollen (phenolics; Liu *et al.*, 2006), or sugar solutions (amygdalin; London-Shafir, Shafir & Eisikowitch, 2003), and feed preferentially on pollen with lower concentrations (but see Liu *et al.*, 2004). Furthermore, honey bees often avoid noxious pollen if other pollen sources are available (London-Shafir *et al.*, 2003; Pimentel de Carvalho & Message, 2004; Liu *et al.*, 2006).

The evolution of repellent or toxic pollen as an anti-theft mechanism probably depends on its effects on primary pollinators. Such pollen should evolve more often when primary pollinators do not consume pollen (e.g. nectar-feeding birds, wind), in which case thief deterrence will not conflict with pollination. However, toxic pollen has also evolved in plants pollinated by pollen consumers (e.g. Cintra, Malaspina & Bueno, 2003; Pimentel de Carvalho & Message, 2004). This apparent paradox may simply be an artefact of toxicity studies that have almost exclusively considered honey bees, which are commercially important, but often non-native, pollinators. Interestingly, Cintra *et al.* (2003) found that anthers of two Brazilian trees, *Stryphnodendron adstringens* (Fabaceae) and *Dimorphandra mollis* (Caesalpiniaceae), were significantly less lethal to native bee pollinators than to introduced honey bees. Such contrasting

effects suggest that pollen toxicity could evolve to deter pollen thieves even for species pollinated by pollen consumers, as long as toxicity affected thieves more than pollen-collecting primary pollinators, especially if thieves can access more palatable options.

(*c*) *Converting thieves into pollinators*

When pollen theft causes pollen limitation within a population, selection through female fitness would not favour anti-theft mechanisms *per se*, as no benefit accrues to specific individuals. Instead, pollen theft should favour traits that cause pollen collectors to serve as pollinators, rather than as thieves. Most pollen collectors pollinate when their foraging brings them into contact with stigmas, but they act as thieves when this does not occur. This is especially true of conditional thieves, who can transfer a few pollen grains to stigmas, even though they generally act as thieves. Two suites of floral traits primarily determine whether pollen collectors steal pollen or pollinate: the separation of pollen-presenting organs from receptive stigmas, and the attractive features of female or female-phase flowers.

In perfect (bisexual) flowers, male and female function can be separated in space (herkogamy; Webb & Lloyd, 1986), or time (dichogamy; Lloyd & Webb, 1986). As herkogamy increases, so does the proportion of visitors whose bodies are too small to contact stigmas as they gather pollen (Table 1). For example, *Trigona* spp. visitors to *Dalechampia magnoliifolia* deposit pollen in flowers with small anther-stigma separation, but not in those with wide separation (Armbruster *et al.*, 1989). Similarly, as dichogamy increases, pollen collectors are more likely to visit only functionally male flowers and avoid female-phase flowers from which the pollen has been either removed (protandry), or not yet been presented (protogyny; Table 1). For example, Ish-Am & Eisikowitch (1993) reported that nectar-collecting honey bees were the primary pollinators of avocado *Persea americana*, whereas pollen-collecting honey bees acted as thieves because they rarely visited female-phase flowers. Of the 51 reported cases of pollen theft from hermaphroditic species that identified why a visitor was a thief (Table 1; each case representing one plant species and one thief species or group), 22 resulted from herkogamy and eight from dichogamy. Thus, flowers with reduced herkogamy and/or dichogamy are more likely to be pollinated than thieved by pollen collectors. However, both traits serve important roles in reducing self-pollination and interference between the sex roles (Lloyd & Webb, 1986; Webb & Lloyd, 1986), which will tend to counteract selection imposed by pollen theft.

In general, the effect of dichogamy on pollen theft will depend on whether pollen collectors visit functionally female flowers, which in turn depends largely on their ability to distinguish female flowers from functionally male flowers (e.g. Ashman *et al.*, 2005). Some hermaphroditic species possess pollen-mimicking structures to attract pollen-collecting pollinators to female-phase flowers, including imitation stamens, and pollen-like style coloration or corolla patterns (Lunau, 2000). Similarly, some species pollinated by pollen-collecting bees produce both

conspicuous 'feeding' anthers (often with dysfunctional pollen) and inconspicuous 'pollinating' anthers (heteranthery; Jesson & Barrett, 2003). Such adaptations could be sufficient to convert pollen thieves into pollinators without compromising mechanisms that reduce self-pollination.

Concealment of pollen within floral structures can also manipulate pollen collectors into pollinating, instead of thieving. If pollen availability cannot be detected without visiting a flower (e.g. poricidal anthers; Buchmann, 1983), pollen collectors may be deceived into visiting female-phase flowers and effecting pollination. Furthermore, structures that conceal pollen may force insects to contact the stigma on their way into a flower. For example, the complex keel flowers of some legumes, which dispense hidden pollen in relatively controlled amounts (Harder & Wilson, 1994) and force most pollen collectors to contact stigmas, have been interpreted as an adaptation for the use of pollen-collecting bees as primary pollinators (Westerkamp, 1997). Nectar guides may also help reduce the incidence of theft by promoting landing and feeding behaviours that enhance stigma contact (Ushimaru, Watanabe & Nakata, 2007). In general, plants pollinated primarily by pollen collectors may be less likely to suffer from pollen theft than those that reward with nectar, as they already possess mechanisms to ensure that pollen collection promotes pollen deposition. For such plants, we expect that most pollen theft involves animals that bypass pollen-dispensing mechanisms, such as pollen-robbing by *Trigona* bees that pierce poricidal anthers (e.g. Renner, 1983; Young, 1983; Gross, 1993).

(2) Sexual-system evolution

In addition to floral traits, pollen theft may influence selection on aspects of plant sexual systems, including the occurrence and form of sexual polymorphism and mechanisms of self-pollination. Dioecy is the most extreme sexual polymorphism, with distinct male and female plants. From a pollen-collector's perspective, pollenless female plants are akin to a distinct, non-rewarding species. As long as pollen-collecting insects can detect pollen (by sensing it directly or recognizing male flowers), they need visit only male plants, and consequently will never deposit pollen on female flowers (Ashman, 2000). Severe and chronic pollen theft should therefore select against complete sexual segregation between male and female plants. Indeed, the high frequency of dioecy on islands that lack native social, pollen-collecting bees, including New Zealand (Godley, 1975), Hawaii (Carlquist, 1974; Sakai *et al.*, 1995), Mauritius (Baker & Cox, 1984) and the Ogasawara Islands of Japan (Abe, 2006), may partially reflect the consequences of relief from pollen theft.

If pollen theft selects against pollenless female plants or flowers, it could promote the evolution of alternative forms of sexual dimorphism, or mechanisms to entice pollen collectors to visit female flowers. For example, Sakai (2001) speculated that androdioecy may have evolved from dioecy in *Castilla elasticus* to attract pollen-feeding thrips to pollinate otherwise unrewarding female plants.

Alternatively, pollen robbery that causes significant floral damage could help maintain female plants in gynodioecious species, or promote dioecy (reviewed in Strauss & Whittall, 2006). Pollen theft may also select for cryptic dioecy, in which female plants produce sterile pollen to attract pollen-collecting pollinators (Anderson & Symon, 1988; Mayer & Charlesworth, 1991; Kawagoe & Suzuki, 2004), or male-mimicry, in which female plants mimic the scent of male flowers, achieving pollination by deception (e.g. figs; Grison-Pige *et al.*, 2001).

Pollen theft could also influence the evolution and maintenance of heterostyly, if pollen foragers visit morphs with exposed, long-level anthers preferentially (e.g. Wolfe & Barrett, 1987; Husband & Barrett, 1992) with sufficient frequency that they reduce intermorph pollination by indiscriminate nectar foragers. In this manner, pollen theft could deter the evolution of heterostyly when it might otherwise be advantageous. Furthermore, recruitment of pollen thieves to the fauna visiting flowers of a functionally heterostylous species could precipitate the breakdown of this sexual system. Beach & Bawa (1980) proposed that a pollinator shift from nectar to pollen foragers could lead to the evolution of dioecy from distyly, with the long-styled morph (with hidden anthers) increasingly acting as females and the short-styled morph (with exposed anthers) acting as males. However, this transition requires that pollen foragers visit long-styled flowers regularly, which is unlikely for pollen thieves, given the inaccessibility of pollen on their short-level anthers. Instead, intense pollen theft could cause the reversion of heterostyly to a monomorphic state with both anthers and stigmas exposed.

Finally, pollen theft could affect the evolution of reproductive assurance in self-compatible species. Delayed selfing, whereby flowers self-pollinate autonomously after opportunities for cross-pollination have largely passed, is arguably the ideal reproductive-assurance strategy because, unlike prior selfing or apomixis, it does not compromise opportunities for outcrossing (Lloyd, 1992; Eckert, Samis & Dart, 2006). However, delayed selfing requires limited pollen removal, so that self-pollen remains to pollinate unfertilized ovules. Obviously, pollen removal by thieves reduces the opportunity for delayed selfing (Vaughton, 1996). Accordingly, selection for reproductive assurance in plants that experience intense pollen theft may favour apomixis (Renner, 1983), or autonomous self-pollination before pollen is exposed to floral visitors (van Kleunen, Fischer & Johnson, 2007).

IV. CONCLUSIONS

(1) Pollen theft influences the ecology and evolution of pollination systems directly and significantly, but strangely has been overlooked despite growing interest in cheating on mutualisms and floral larceny. Pollen theft may contribute to many aspects of pollination biology, including the widespread occurrence of pollen limitation, and may cause selection for unusual floral adaptations, such as cryptic or toxic pollen. Despite formidable methodological problems in studying pollen theft, including the difficulties of quantifying pollen (rather than gene) dispersal and of manipulating pollen theft

at the population level, it will likely receive much more future attention because of its impacts on many fundamental aspects of plant reproduction.

(2) Both the frequency of pollen theft and its spatial and temporal variation are very poorly known. Pollen theft probably occurs much more frequently than suggested by the existing literature (summarized in Table 1), because pollination studies typically focus on effective pollinators. Quantification of temporal and spatial variation in pollen theft will enable assessment of its role in the selection of plant reproduction, whereas more complete documentation of its occurrence will clarify the associations revealed by this review, namely whether eusocial bees act most commonly as thieves and plant species with pronounced separation of sex roles in space and/or time are most susceptible to theft.

(3) Pollen theft can clearly impede plant reproduction (Table 2), but the frequency of this effect remains unknown. More complete tests of the effects of pollen theft on plant reproduction, especially direct manipulation of thief abundance, are needed to assess its general ecological and evolutionary importance. Of particular urgency from a conservation perspective is the need to understand the ecological consequences of pollen theft by exotic eusocial bees for native plant species. Finally, the unknown importance of pollen theft compared to that of other interactions that can limit reproductive potential, such as seed and seedling predation, is one aspect of a general lack of comprehensive studies that examine reproduction both before and after seed production.

(4) According to our definition, whether pollen foragers that deposit few grains on stigmas act as inefficient pollinators or conditional pollen thieves depends on the composition and pollination effectiveness of other flower visitors. Furthermore, pollen thieves can act simultaneously as antagonists for some plant species, but as mutualists for others. Indeed, the possibility that a plant species might maintain populations of animals that act as its 'thieves', but as pollinators for other species that flower at different times (Baker *et al.*, 1971) awaits examination. Thus, both the incidence and effects of pollen theft should often depend on the community context within which it occurs. This context is a poorly considered aspect of pollination as a whole, and warrants greater attention in future studies of pollen theft.

(5) We have interpreted various aspects of flowers and pollen as potential pollen-thief deterrents, but the actual role of such traits in preventing or mitigating pollen theft remains to be tested. One of the least explored and most interesting of these possible adaptations is repellent, toxic or inedible pollen. If noxious pollen evolves specifically to deter thieves, rather than as a pleiotropic effect of vegetative defences, it should be more common in plants whose primary pollinators do not consume pollen. Even if toxic or repellent pollen evolves initially through pleiotropy, if it serves to deter thieves then pollen-consuming pollinators should be less susceptible to the deterrent (chemical or structural) than the primary pollen thieves, and individual plants with more deterrent pollen should sire more offspring than less deterrent individuals.

(6) By differentially impacting floral morphs with more accessible pollen, pollen theft has the potential to influence the evolution of polymorphic sexual systems, but these influences have not been explored empirically. The possibilities that dioecy evolves more frequently in the absence of social pollen collectors and that cryptic dioecy is associated with the presence of pollen thieves are particularly intriguing. Situations involving introduced pollen thieves, especially honey bees, are prime candidates for exploring this aspect of pollen theft (e.g. Sjöström & Gross, 2006).

(7) As one of the richest sources of protein produced by plants, pollen is a valuable resource for animals. Animals that visit flowers to consume or collect pollen are self-motivated and do not act specifically to promote pollination; when their foraging activity is mismatched in space or time with receptive stigmas, traits that otherwise promote pollination instead enable theft. Given the likely frequency and potential ecological and evolutionary consequences of such mismatches, pollen theft warrants broader consideration and analysis.

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