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The impact of floral larceny on individuals, populations, and communities

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Abstract Many insects and other animals that visit flowers are not mutualistic pollinators, but rather "behavioral robbers" which pierce flowers to extract nectar, and "thieves" which enter flowers in the normal way but provide little or no pollination service. Although the study of floral larceny has grown rapidly in the last two decades, the importance of larceny for individual fitness and for population- and community-level phenomena is only now becoming apparent. Here we synthesize the current understanding of floral larceny by reviewing and re-analyzing existing published data, by presenting new data of our own, and by suggesting avenues of further research. First, we perform a meta-analysis on existing studies, which shows that larceny has an overall detrimental effect on female reproductive success of plants, and that effect size depends on the types of robbers, thieves, and pollinators that interact as well as on the reproductive biology of the plant. This quantitative analysis improves upon a recently published qualitative analysis of larceny and plant fitness. Next, we discuss the possibility that larcenists and pollinators can select in different directions on floral traits, possibly contributing to the standing variation in floral phenotypes that is observed within natural populations. Larceny has the potential to affect plant population dynamics, so long as offspring recruitment and survival depend on seed production, a point we illustrate with data from the montane herb *Ipomopsis aggregata*. Our studies of this species also show how larcenists may influence community-level dynamics, by linking plant species that they rob or by influencing other plant species through altered behavior of shared pollinators. Population- and community-level effects of larceny, and their possible roles in stabilizing pollination food webs, provide rich prospects for future research.

Keywords Floral larceny · Food webs · Indirect effects · Pollination · Population dynamics

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Introduction

Most flowering plants depend on animals for pollination. Insects and other animals pollinate 90% of some 300,000 species of angiosperms worldwide (Tepedino 1979; Buchman and Nabhan 1996), an end-product of >100 million years of evolution and adaptive radiation by both the animals and plants (Herre et al. 1996). But this evolutionary history began with interactions in which the animals were opportunistic or obligatory herbivores (Crepet 1983), and modern-day mutualisms between plants and pollinators are not inherently cooperative. Instead, they represent compromises between the requirements of plants for sexual reproduction versus those of pollinators for food and other floral resources (e.g., Darwin 1876; Waser and Price 1983, 1998; Westerkamp 1991; Kearns et al. 1998).

These compromises can be exploited. Nowhere is this clearer than in the phenomenon of floral larceny, an umbrella term covering a range of behaviors by which animals obtain rewards from flowers in ways that appear to effect no pollination and/or to damage the flowers. Here we follow Inouye (1980) in broadly classifying larcenists as "behavioral robbers" (hereafter "robbers"), who pierce flowers to extract nectar rather than legitimately

entering them, and "thieves", who enter flowers as pollinators do but transfer little or no pollen, usually due to a mismatch with the flower's morphology.

Recognition that flower visitors include facultative and obligatory larcenists dates at least to Herman Müller (1873) and Charles Darwin (1876), who discussed robbing behavior in detail over a century ago. Since then, evidence for the ubiquity of robbing and thievery has accumulated. However, a clear picture of its importance for individual fitness and for population- and community-level dynamics is just beginning to emerge. Here we contribute to this picture by reviewing and re-analyzing existing published data, by presenting some new data of our own, and by suggesting avenues for further research.

Floral larceny and plant reproduction

Robbers and thieves are widespread (Maloof and Inouye 2000). In spite of this, these cheaters generally have not been considered critical to plant reproduction (e.g., Rust 1979; Newton and Hill 1983; Norment 1988; Goulson et al. 1998). Recently, this assumption has been challenged, and literature surveys demonstrate that the net effects of cheating for female plant reproduction can be negative, positive, or neutral (Inouye 1983; Maloof and Inouye 2000). The *direct negative* effects of nectar robbing, via damage to reproductive organs (Galen 1983, 1999) and/or antagonistic interactions in which robbers drive away legitimate pollinators (Roubik 1982), are easy to envision. Conversely, some nectar robbers actually have a *direct positive* effect by pollinating at least a fraction of the flowers they rob (citations in Maloof and Inouye 2000). Pollination in such cases ranges from occasional and accidental at one extreme, to regular and "intentional".

To understand this range of behaviors of flower visitors, we make the assumption that all the behaviors occur because they are efficient ways to obtain resources. This leads to the prediction that larceny will be obligatory for an animal in some cases and, in other cases, facultative, depending on the rewards provided in the flowers visited and on the rest of the floral environment (and hence other resources) available to that animal. Furthermore, it may be efficient for an animal to behave as a robber or thief with respect to one floral resource and behave in a "legitimate" fashion with respect to another. For example, bumblebees systematically rob older flowers of *Mertensia paniculata* which contain nectar, but buzz-pollinate young flowers which contain only pollen (Morris 1996). Or, the intentional collection of one resource may engender pollination (this is our meaning of "intentional" in the previous paragraph, rather than any implication that animals "intend" to assist plant reproduction). For example, female carpenter bees pierce flowers of ocotillo to obtain nectar, but pollinate while collecting pollen from the same flowers (Waser 1979). In short, close inspection can reveal combinations of behaviors and net fitness effects that are unexpected if one presumes that

Table 1 Studies used in the meta-analysis, and their characteristics

Larcenists	Primary pollinators	Plant species	Reference
Ants			
Multiple species	*Danus* spp.	*Asclepias curassavica*	Wyatt (1980)
Multiple species	Multiple insects	*Asclepias syriaca*	Fritz and Morse (1981)
Formica neorufibarbus gelida	*Bombus* spp.	*Polemonium viscosum*	Galen (1983, 1999)
Multiple species	Multiple insects	*Frasera speciosa*	Norment (1988)
Bumblebees (*Bombus*)			
B. hypocrita sapporensis	*B. hypocrita*	*Corydalis ambigua*	Higashi et al. (1988)
Multiple species	*Bombus* spp.	*Mertensia paniculata*	Morris (1996)
Multiple species	*Bombus* spp.	*Symphytum officinale*	Goulson et al. (1998)
B. occidentalis	Hummingbirds	*Ipomopsis aggregata*	Irwin and Brody (2000)
Multiple species	Multiple insects	*Anthyllis vulneraria*	Navarro (2000)
Birds			
Diglossa baritula	Hummingbirds	*Salvia mexicana*	Arizmendi et al. (1996)
D. baritula	Hummingbirds	*Fuchsia microphylla*	Arizmendi et al. (1996)
Phrygilus patagonicus	*Sephanoides galeritus*	*Fuchsia magellanica*	Traveset et al. (1998)
Trigona bees			
Multiple species	Hummingbirds	*Pavonia dasypetala*	Roubik (1982)
Multiple species	Hummingbirds	*Quassia amara*	Roubik et al. (1985)
Carpenter bees (*Xylocopa*)			
X. californica	Hummingbirds and insects	*Fouquieria splendens*	Waser (1979)
X. violacea	Multiple insects	*Petrocoptis grandiflora*	Guitián et al. (1994)
Butterflies			
Multiple species	Multiple insects	*Centaurea solstitialis*	Agrawal et al. (2000)
Wasps			
Vespula maculifrons	*Bombus* spp.	*Impatiens capensis*	Rust (1979)

animals act only in stereotypic ways that can be placed into a few convenient categories.

Additionally, robbers and thieves may have more subtle *indirect* effects on plant fitness, for example by altering the interaction between plants and pollinators (interaction modifications, sensu Wootton 1993). The result may be to decrease plant fitness if larceny reduces floral rewards sufficiently for pollinators to avoid a plant or to desert it after a brief visit (Irwin and Brody 1998; 2000). Or the result may be to increase fitness if each pollinator visits fewer flowers per plant, so long as there is a sufficiently high fitness cost of within-plant selfing (see Galen and Plowright 1985; Klinkhamer and de Jong 1993; Hodges 1995).

What is the empirical evidence for these various positive and negative, direct and indirect effects of larceny? Maloof and Inouye (2000) reviewed nectar robbing (but not thievery) and concluded that robbers are about equally likely to increase or decrease plant fitness. However, their analysis did not take into account the *magnitude* of fitness effects and, therefore, suffers from a form of "vote counting" (Gurevitch and Hedges 1993) in which a judgment of positive and negative effects is based only on the statistical significance of outcomes and on authors' summaries. In contrast, we contend that sample sizes and statistical power must also be considered in any such evaluation.

To quantitatively examine the effects of both robbing and thievery on female reproductive success of plants (fruit or seed set), we performed a meta-analysis using the methods of Gurevitch and Hedges (1993). We could not analyze male reproductive success of plants (seeds sired) because, to our knowledge, only one published study has examined how this measure responds to robbing (Irwin and Brody 2000). We included only studies in which larceny was variable among flowers, plants, or populations and for which the authors reported the effects of robbing on the reproduction of individual flowers or entire plants. A search of Biosis from 1979 to 2000 using the key words cheater, nectar robber, nectar thief, and floral larceny yielded 17 such studies, all involving larceny of nectar (Table 1).

For each study, we calculated an effect size (d) that expresses the difference in mean female reproductive success in plants or flowers that did versus did not experience larceny, divided by their pooled SD. A positive effect size indicates positive effects of robbing and vice versa. An absolute value of 0.2 is considered a small effect, 0.5 medium, 0.8 large, and ≥1.0 very large (Cohen 1969). We calculated the cumulative effect size across studies to determine the overall impact of larcenists and then compared effect sizes across studies of different types of larcenist-pollinator combinations (bird-bird, insect-bird, and insect-insect), different types of larcenists (robber versus thief), different research approaches (experimental versus natural larceny), and different interactive outcomes (positive versus negative effects of robbing). These comparisons were analyzed statistically using a between-class homogeneity statistic (Q_b) which has a χ^2 distribution with df equal to the number of classes minus one (Gurevitch and Hedges 1993). To compare studies that yielded positive versus negative effect sizes, we used the absolute value of effect size to compare the magnitude of effect size rather than the direction.

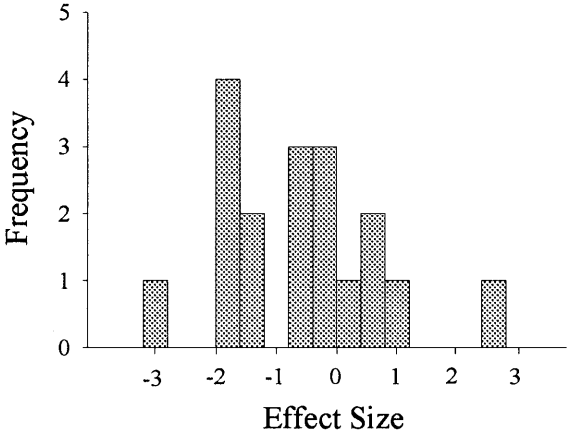

Fig. 1 Frequency distribution of effect sizes from a meta-analysis on the effect of floral larceny on female plant reproduction. *Negative values* indicate negative effects of larceny on reproduction, and vice versa

Overall, floral larceny had a weak but negative effect on female reproductive success (d=–0.27). Individual values of d ranged from –3.01 to +2.74 (Fig. 1). On average, studies finding negative effects of floral larceny reported stronger fitness consequences than those finding positive effects (Fig. 1). The type of larcenist-pollinator combination had a significant impact (Q_b=17.25, df=2, P<0.0001). In plants that were bird-pollinated, insect larcenists had a weak negative effect (d=–0.25) on female reproduction, while avian larcenists had a relatively strong negative effect (d=–1.07). For insect-pollinated plants, floral larceny by other insects had a weak positive effect (d=+0.23), apparently driven by cases in which robbers pollinate flowers from which they steal nectar, either accidentally or "intentionally", as described above (see also Maloof and Inouye 2000). We found no difference in the effect of nectar robbers versus nectar thieves (Q_b=2.01, df=1, P>0.05). Finally, we found significantly larger effect sizes in studies that manipulated floral larceny experimentally than in those that were purely observational (d=0.87 versus 0.25; Q_b=32.06, df=1, P<0.0001).

Several factors may contribute to this last result. Studies that did not manipulate robbing often quantified its effects at the flower level (i.e., comparisons of robbed versus unrobbed flowers); whereas, studies that experimentally manipulated robbing quantified effects at the plant level (i.e., comparisons of plants with high versus low robbing). Comparisons at the flower level might mask important effects. For example, pollinators might not discriminate between robbed and unrobbed flowers on the same plant, but might discriminate between plants with high versus low robbing. Furthermore, studies that

did not experimentally manipulate robbing often failed to report the level of robbing received by the entire plant. Comparing robbed and unrobbed flowers on plants that have variable levels of robbing may render per-flower effects uninterpretable.

In summary, a quantitative meta-analysis suggests that floral larceny overall has a weak negative effect on female reproductive success of plants. The effect seems dependent on the types of robbers, thieves, and pollinators that interact (in agreement with Maloof and Inouye 2000), and on the reproductive biology of the plants. To go beyond these statements, more studies must experimentally manipulate floral larceny to explore the subtleties of direct and indirect interactions, averaged across temporal and spatial variation. Only this kind of effort will allow us to establish clear trends.

Floral larceny and natural selection

The evolution of floral traits surely must be understood, in part, with reference to pollinators. But from the plant's perspective, the selection environment includes larcenists, and other plant enemies, as well as mutualists. To date we have precious few estimates of phenotypic selection by larcenists.

Ants, *Formica neorufibarbus gelida*, steal nectar from the bumblebee-pollinated alpine skypilot, *Polemonium viscosum*, in the process damaging female parts of flowers and rendering them barren (Galen 1983, 1999). These ants prefer flowers with long, broadly flared corollas. However, such flowers are also chosen more often by bumblebee pollinators. Similarly, the bumblebee *Bombus occidentalis* robs nectar from hummingbird-pollinated scarlet gilia, *Ipomopsis aggregata*, causing a 50% loss in both male and female reproductive success (Irwin and Brody 2000). *B. occidentalis* workers emerge in midsummer, so plants that bloom later in the season suffer higher levels of robbing than those that bloom early (R. E. Irwin, unpublished data). At the same time, however, later flowering individuals of *I. aggregata* may receive higher levels of pollination because they avoid competition with an earlier flowering species for the services of hummingbird pollinators (Waser 1978).

In both of these examples, plants face tradeoffs in attracting pollinators while avoiding nectar robbers. In the case of skypilot, robbing ants and pollinating bumblebees both prefer plants with broadly flared flowers and, therefore, select in opposite directions on corolla flare. In the case of scarlet gilia, plants that bloom mid-season experience high levels both of robbing and of pollination; here robbers and pollinators may select in opposite directions on flowering phenology. The net direction and magnitude of selection will likely depend on the relative abundances in space and time of robbers and pollinators.

We emphasize here the possibility that natural selection from larcenists can oppose selection from pollinators. If so, we may have one explanation for the observation that substantial variation in floral phenotype is maintained in natural populations (e.g., Campbell 1991; Armbruster et al. 1999). However, we also must admit our ignorance at this point – relatively few studies are in hand that make formal estimates of phenotypic selection by which we might evaluate how often larcenists and pollinators select in different or similar directions, and on what traits. Take heart, students looking for projects; there is plenty to do!

Floral larceny and plant population dynamics

For cheaters to affect plant populations, they must influence whole-plant seed production, and there must be a direct link between seed production and subsequent population size. These links are only now beginning to be explored (Eriksson and Ehrlén 1992; Turnbull et al. 2000). Most studies to date simply assume that increases or decreases in seed production will translate into subsequent numbers of reproducing offspring one generation later. This assumption may be reasonable (Ackerman et al. 1996; Juenger and Bergelson 2000), but it is not automatically so since other factors, such as limited safe sites for seedling germination, can override seed numbers in determining population size (Crawley and Nachapong 1985; Eriksson and Ehrlén 1992).

A few recent studies demonstrate that plant enemies other than robbers have population-level impacts. The spatial pattern of seed dispersal by birds accurately predicted the subsequent location of seedlings of a Mediterranean tree in a shrubland site, but not in a forest site, where postdispersal seed predation played a larger role (Herrera et al. 1994). Individuals of Platte thistle (*Cirsium canescens*) that were protected experimentally from inflorescence-feeding insects produced more seeds, seedlings, and flowering adults than those not protected (Louda and Potvin 1995). In bush lupine (*Lupinus arboreus*), seedling recruitment was limited in some areas by the removal of seeds by granivores (Maron and Simms 1997).

We know of only one study system – that of the perennial wildflower *Ipomopsis aggregata* and its nectar-robbing bumblebee, *Bombus occidentalis* – for which both nectar robbing and seed input have been experimentally manipulated and subsequent population growth examined. As previously noted, heavy robbing by *B. occidentalis* results in a 50% decline in seed production by *I. aggregata*. In experimental plantings, a 50% reduction in seed input indeed yielded virtually a 50% reduction in numbers of new seedlings and first-year juveniles (Waser et al. 2000). Because *I. aggregata* is a semelparous perennial that flowers in some cases only after 7 years or more, we cannot claim that these results are final. However, they do suggest that we may ultimately be able to show for this species that robbing influences the next generation of plants. To draw wider conclusions about larceny and population dynamics, we will have to wait for more studies that link reproductive success with offspring demography.

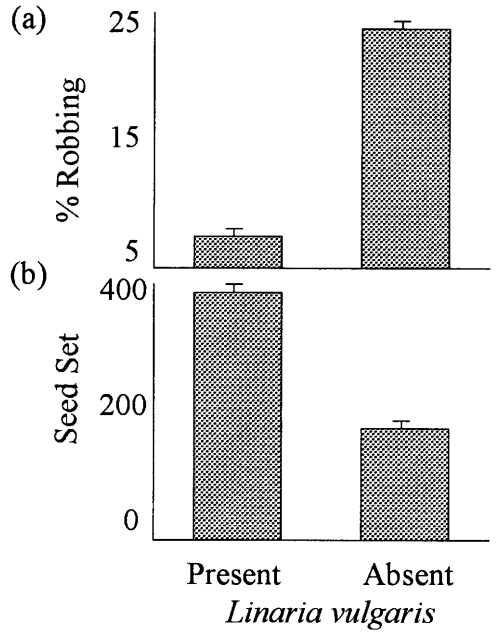

Fig. 2 *Ipomopsis aggregata* mean percent robbing per plant (+SE) (**a**), and mean seed production per plant (+SE) (**b**), in two sites with and three sites without *Linaria vulgaris*, a sympatric species that shares a common nectar-robbing bumblebee. Pooled across sites, the presence of *L. vulgaris* significantly reduced robbing of *I. aggregata* (ANOVA on arcsine square-root transformed values: $F_{1,159}$=19.1, P<0.0001) and significantly increased seed production of this species (ANOVA on natural log-transformed values: $F_{1,159}$=40.1, P<0.0001)

Floral larceny and community ecology

The interactions between a plant species, its pollinators, and its larcenists are embedded in a larger web of interactions. Robbed plants grow sympatrically with other plant species that share larcenists and/or pollinators. If two or more plant species share the same nectar robber, they may facilitate each other's robbing, (*associational susceptibility*, sensu Huntly 1991). One variant, akin to pollinator facilitation (sensu Waser and Real 1979), is *sequential facilitation* in which sequentially flowering species facilitate each other's robbing through mutual support of robber populations. Alternatively, if robbers prefer one species, the less-preferred may benefit – an outcome akin to *associational resistance* to herbivores (sensu Boucher 1985; Wahl and Hay 1995). Finally, community members may have no effect on each other if robbing intensity is independent of plant density and robbers show little or no preference for any species.

We know of no published studies to date that explore such interactions, but have begun studies of our own comparing robbing rates and female reproductive success of *Ipomopsis aggregata* in populations with and without *Linaria vulgaris*, a co-occurring introduced species that is also robbed of nectar by *Bombus occidentalis*. Robbing rates of *I. aggregata* were 68% lower in the presence of *L. vulgaris* than in its absence (Fig. 2A), with *L. vulgaris* receiving 60% more robbing than *I. aggregata* where the two species grew together. Hence *L. vulgaris* appeared to have an *indirect* positive effect on *I. aggregata* by luring away robbers, as indicated by higher seed set of *I. aggregata* when it grew with *L. vulgaris* (Fig. 2B). However, the long-term outcome of the interactions between *I. aggregata* and *L. vulgaris* will also depend on the degree to which each population is seed limited, and on the extent of interspecific competition for space, aspects which we are now examining.

Within a community, plants often compete for pollination services (Waser 1983). How might floral larceny affect this interaction? Suppose that two plant species compete for pollination services and one loses floral rewards (e.g., nectar) to larcenists. Pollinators may avoid foraging on the less-rewarding species and so increase the reproductive success of the unrobbed species – an *indirect* positive effect through behavioral modification (sensu Wootton 1993) of shared pollinators. Once again, *I. aggregata* provides a possible example. Broad-tailed and rufous hummingbirds prefer *I. aggregata* as a nectar source when it co-occurs with paintbrush, *Castilleja linariaefolia*, another hummingbird-pollinated plant. However, of the two, *B. occidentalis* robs only *I. aggregata*. In so doing, *B. occidentalis* can shift the preference of hummingbirds toward *C. linariaefolia*. Preliminary results suggest that seed set of *C. linariaefolia* is higher in the presence of robbed *I. aggregata* than in the presence of unrobbed *I. aggregata* (A. K. Brody and R. E. Irwin, unpublished data).

These examples illustrate some of the ways in which robbers may influence community-level dynamics. In addition, robbers may affect the growth or stability of pollinator populations and the relative importance of one group of pollinators versus another. The complete suite of community-level effects of nectar robbers is so far unstudied.

Floral larceny and stability of food webs

Evidence is accumulating that the interactions between flowers and their animal visitors are web-like in structure, at least in temperate ecosystems (e.g., Petanidou and Ellis 1996; Memmott 1999; J. Memmott and N. M. Waser, unpublished data; R. Alarcón, unpublished data). Thus, the flowers of many plant species in a community are visited by a diverse array of insects and other animals, and conversely, many animals visit a diverse array of plant species. Indeed, even morphologically specialized flowers often are visited by a variety of animals (e.g., Mayfield et al. 2001).

At one extreme, all flower visitors might be pollinators, and flower-visitation webs could perfectly correspond to pollination webs. But the more likely truth is that some flower visitors are larcenists, even leaving aside any behavioral robbers. Thievery by some flower visitors may be obligatory; these animals simply do not "fit" flowers morphologically and so obtain rewards

without transferring pollen (e.g., Wicklund et al. 1979). Or thievery may be facultative in the sense that the fitness value of visits to the plants depends on the presence or absence of other potential pollinators (e.g., Thompson and Pellmyr 1992), and possibly other factors as yet unexplored.

Is it possible, then, that thieves comprise a moderate to large part of flower visitation webs (e.g., Ollerton 1996)? If so, these animals should not be excluded from further consideration: witness their important roles, as outlined above, in plant reproduction, floral evolution, population dynamics, and community-level interactions. Furthermore, thieves may play a role in the stability of communities they belong to. Various aspects of stability, such as spatial and temporal fluctuation in species' abundances, may depend critically on the richness of interactions between trophic levels (in this case, between primary producers and primary consumers) as well as on the strength and direction of these interactions. For example, theoretical models predict that weak negative interactions reduce temporal variance (McCann et al. 1998) but increase spatial variance (Benedetti-Cecchi 2000) in species' abundances. Furthermore, models of two trophic levels suggest that negative interactions are more stabilizing than positive interactions (McPhearson and Jiang 2000). Hence, both high connectance of flower-visitor webs, which will reduce the strength of many individual interactions, and the presence of thieves (i.e., negative interactions) in the webs, may contribute to the long-term persistence of these systems.

Conclusions and future prospects

The study of floral larceny has grown rapidly in the last two decades (Fig. 3), but our understanding of its importance to individual plants, and to populations and communities, remains rudimentary. A growing number of reports suggests that larcenists can have positive, neutral, and negative effects on plant reproductive success, with weak negative effects predominating and with variations around this theme depending on the types of larcenists and pollinators involved. Larcenists can influence floral evolution in concert or in opposition to selection by pollinators. And floral larceny may have impacts on plant-population growth and community-level interactions. Finally, larcenists may influence the stability of the web of interactions in which they are embedded.

Exciting challenges remain. More experimental studies are needed to determine the effects of floral larceny on male as well as female reproductive success, and on the evolution of floral traits. Such studies should move beyond a focus on behavioral robbers to include the more subtle thieves that enter flowers as pollinators do. For example, it will be interesting to determine whether floral phenotypes evolve to exclude thieves, as long assumed in pollination biology (e.g., Straw 1956). This might be approached by comparing phenotypic selection in the presence of all flower visitors versus selection with apparent thieves excluded. The effects of larceny on plant-population and plant-community dynamics present additional open fields for study. Last but not least, it will be valuable to characterize flower visitation webs in a variety of ecosystems (temperate, tropical) and ecoregions, and to determine what fractions of the interactions are larcenous. The prevalence of floral larceny in flower visitation webs is likely to provide a greater understanding of how species are ecologically and evolutionarily linked in biological communities, and on how these communities will change with natural and anthropogenic perturbation.

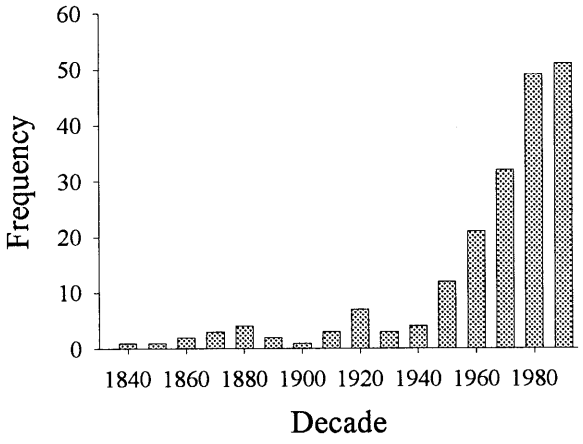

Fig. 3 Numbers of studies on floral larceny published per decade, from the 1840s to the 1990s, gleaned from a survey of the literature

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