

Review

Novel Consequences of Bird Pollination for Plant Mating

Siegfried L. Krauss,^{1,2,*,@} Ryan D. Phillips,^{1,2,3} Jeffrey D. Karron,⁴ Steven D. Johnson,⁵ David G. Roberts,^{1,6} and Stephen D. Hopper⁶

Pollinator behaviour has profound effects on plant mating. Pollinators are predicted to minimise energetic costs during foraging bouts by moving between nearby flowers. However, a review of plant mating system studies reveals a mismatch between behavioural predictions and pollen-mediated gene dispersal in bird-pollinated plants. Paternal diversity of these plants is twice that of plants pollinated solely by insects. Comparison with the behaviour of other pollinator groups suggests that birds promote pollen dispersal through a combination of high mobility, limited grooming, and intra- and interspecies aggression. Future opportunities to test these predictions include seed paternity assignment following pollinator exclusion experiments, single pollen grain genotyping, new tracking technologies for small pollinators, and motion-triggered cameras and ethological experimentation for quantifying pollinator behaviour.

Plants and Pollinators

Mating is a key microevolutionary process, influencing the movement of genes in space and their transmission through time. An understanding of mating patterns is fundamental to evolutionary biology [1] and increasingly critical for the conservation and management of populations and species impacted by environmental change [2–4]. Plant **mating systems** (see [Glossary](#)) are influenced by intrinsic factors, such as floral morphology and self-compatibility, and by extrinsic factors, such as pollinator mobility and foraging behaviour [5,6].

Almost 90% of the 400 000 flowering plant species worldwide rely on animals for **pollination** [7], the behaviour of which has profound effects on plant mating [8,9]. Food-foraging pollinators are predicted to conform to **optimal foraging** theory, whereby energetic costs during foraging bouts are minimised by moving preferentially between nearby flowers, resulting in **geitonogamy**, leptokurtic pollen dispersal and **correlated paternity** [10,11]. However, from the perspective of the plant, longer-distance pollen dispersal decreases the likelihood of inbreeding, meaning that pollinators that move greater distances, skip more intervening flowers, or show departures from optimal foraging may result in higher offspring fitness for the plant.

Recent studies have highlighted novel mechanisms of pollinator attraction, and led to the discovery of an increased diversity of animal taxa known to transport pollen, especially in the Southern Hemisphere [12–15]. The diversity of pollination strategies among plants is likely to be reflected in a similarly diverse range of patterns of pollen dispersal. Resolving the consequences of different pollination strategies for pollen dispersal across multiple spatial scales is important for understanding the fitness advantages and, thus, evolution of particular strategies. Here, we focus on bird pollination, a strategy that has been at the forefront of investigations to

Trends

Recent molecular studies of mating patterns in flowering plants are providing important insights into the ecological genetic consequences of bird pollination.

These studies show that bird-pollinated plants are typically sired by nearly twice as many mates as are insect-pollinated plants.

High mobility, limited grooming, and intra- and interspecies aggression are likely to be key behavioural characteristics of birds that facilitate pollen carry-over and promote high mate diversity in the plants that they pollinate.

¹Kings Park and Botanic Garden, Botanic Gardens and Parks Authority, Fraser Avenue, Kings Park, WA 6005, Australia

²School of Plant Biology, University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia

³Ecology and Evolution, Research School of Biology, The Australian National University, Canberra, ACT 2601, Australia

⁴Department of Biological Sciences, PO Box 413, University of Wisconsin-Milwaukee, Milwaukee, WI 53201, USA

⁵School of Life Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville, Pietermaritzburg 3209, South Africa

⁶Centre of Excellence in Natural Resource Management and School of Plant Biology, University of Western Australia, 35 Stirling Terrace, Albany, WA 6330, Australia

*Correspondence: skrauss@bgpa.wa.gov.au (S.L. Krauss).
 @Twitter: @SiegyK

understand floral adaptation to pollinators and mechanisms underpinning transitions between pollination strategies [16–19].

Bird Pollination: What Birds, What Plants, and Where

Although most flowering plants are insect pollinated, more than 900 bird species pollinate members of ca. 500 of the 13 500 vascular plant genera [19–22], making bird pollination one of the most taxonomically widespread pollination strategies. The four main lineages of pollinating birds are hummingbirds (ca. 340 spp.; Trochilidae), sunbirds (ca. 132 spp.; Nectariniidae), honeyeaters (ca. 180 spp.; Meliphagidae), and lorikeets (ca. 55 spp.; tribe Loriini of the Psittaculidae), although there are also specialist nectarivores in the asities (Philepittidae), sugarbirds (Promeropidae), Hawaiian honeycreepers (Fringillidae), white-eyes (Zosteropidae) and Platycercini parrots that make locally important contributions to pollination (Figure 1) [22–24]. In some regions, there are also guilds of plants with readily accessible rewards that are pollinated primarily by short-billed birds, such as weavers, bulbuls, and starlings, that are only occasionally nectarivorous [22,25].

All of the major families of nectarivorous birds reach their highest diversity in the tropics and Southern Hemisphere, in particular the Andes and central American mountains (hummingbirds), African and Asian tropics (sunbirds), and eastern Australia and New Guinea (honeyeaters and lorikeets) (Figure 2). Interestingly, the diversity of bird-pollinated plants appears not to correlate strongly with nectarivorous bird diversity. For example, both the Southwest Australian Floristic Region and the Greater Cape of South Africa have diverse bird-pollinated floras, but a relatively low diversity of nectarivores compared with other regions on their respective continents [23,24,26–28].

While some plants are pollinated by one or a few bird species, most nectarivorous birds, including those with highly exaggerated bill morphology, feed on a range of plant species [24,29]. Plants that are primarily pollinated by birds often have red flowers, elongated floral tubes, and copious amounts of dilute nectar [19,24]. However, a range of other colours (e.g., typically orange and yellow, but also white, violet, green, and black) and morphologies are exhibited by a lesser diversity of bird-pollinated species [19,24,30]. In many cases, bird-pollinated flowers are also visited by other pollinator groups, particularly bees and nonflying mammals [22,31,32], although the morphological adaptations to bird pollination often mean that insect visitors are comparatively ineffective at removing and depositing pollen [33]. This has been demonstrated by the sharp decline in seed production that is typically observed when birds, but not insects, are experimentally excluded from both bird-adapted flowers [33,34] and, remarkably, in some seemingly nonbird-adapted flowers [22]. Zygomorphy and tubular flowers appear to be preadaptations that favour the evolution of bird pollination [19], with bird pollination more commonly evolving from bee pollination than it does from other strategies [35].

The diversity of bird species involved in pollination means that there are often multiple avian pollination niches to which plants can adapt. For example, in Australia, it is common to have plants with long tubular flowers pollinated by long-beaked honeyeaters co-occurring with *Eucalyptus* (Myrtaceae), which has open-faced flowers pollinated by a range of honeyeaters and lorikeets [36]. Studies in South America and Africa suggest that more than one bird pollination system occurs in a particular community, and that further niche partitioning occurs along a flowering time axis [37]. Consequently, mating outcomes for plants may vary according to the type of birds involved as well as interactions among plant species [37,38].

Bird Pollinator Behaviour

Given the variation in foraging and social behaviours between different groups of nectarivorous birds, there is expected to be substantial variation in the ecological and evolutionary

Glossary

Correlated paternity: the degree to which seed from the same fruit or plant shares the same male parent. The inverse provides an estimate of the effective number of sires.

Geitonogamy: transfer of pollen from one flower to another on the same plant.

Mating system: describes patterns of syngamy between and within individuals, or equivalently, who shares parentage with whom in a population. Measuring it ideally takes the form of a complete enumeration of matings.

Multiple paternity: offspring being sired by more than one male pollen donor.

Optimal foraging: describes the foraging behaviour exhibited by animals that minimises time and energy expenditure in the search for food.

Outcrossing rate: proportion of seeds that are the product of mating between individual plants; estimated using molecular markers.

Pollen carryover: the proportion of pollen removed from a focal flower that is deposited on each successive flower in a visitation sequence.

Pollen grooming: the removal of pollen by a pollinator from its body, for which the timing and frequency will impact pollen carryover.

Pollen vector: an external force that transfers pollen (e.g., wind, water, or an animal).

Pollination: the reception by a stigma of a pollen grain contributed either from the same plant (self-pollination) or from a different plant (cross-pollination).

Self-incompatibility: inability of a hermaphroditic plant to produce seeds following self-pollination due to a physiological barrier acting before fertilisation.

Territoriality: where aggression is used by an animal to behaviourally dominate others to defend the resources associated with a particular area.

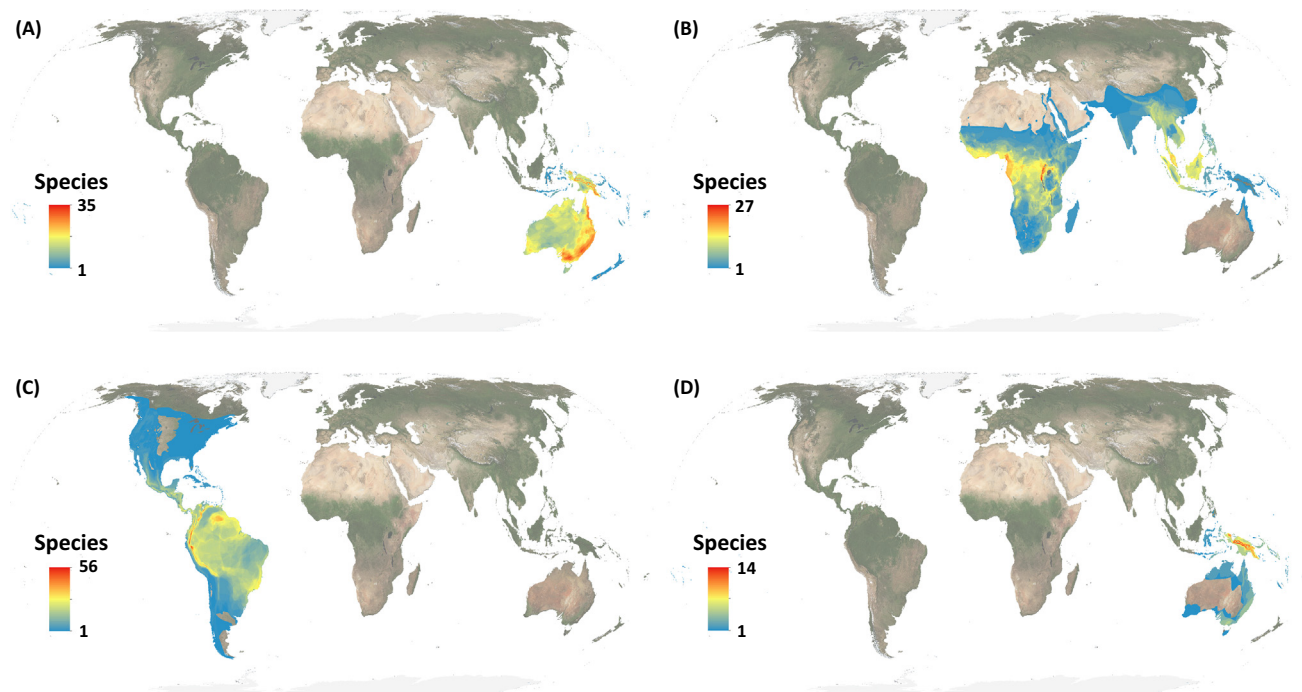
Trapping: the travelling by animals between small, scattered nectar resources, which are not defended against other floral visitors. These resources are visited by following a regular route and a particular sequence of plants.



Trends in Plant Science

Figure 1. Examples of Nectarivorous Birds Visiting Flowers and Effecting Pollination. (A) New Holland honeyeater (*Phylidonyris novaehollandiae*) on *Anigozanthos flavidus* (Western Australia); (B) tawny-bellied hermit (*Phaethornis symmatophorus*) visiting *Fuchsia* sp. (Ecuador); (C) copper-rumped hummingbird (*Amazilia tobaci*) on *Calliandra californica* (Mexico); (D) eastern spinebill (*Acanthorhynchus tenuirostris*) on *Telopea speciosissima* × *T. mungaensis* (Eastern Australia); (E) dark-capped bulbul (*Pycnonotus tricolor*) on *Aloe vryheidensis* (South Africa); (F) female amethyst sunbird (*Chalcomitra amethystine*) on *Aloe maculata* (South Africa); (G) rainbow lorikeet (*Trichoglossus haematodus*) on *Corymbia maculata* (Western Australia). Reproduced, with permission, from (A) Myles Menz, (B,C) Herbert Stärker, (D) Suzi Bond, (E,F) Steve Johnson, and (G) Steve Hopper.

consequences of bird pollination. Among hummingbirds, there is an apparent dichotomy between those that defend small territories within which focal nectar sources are repeatedly visited, and trap-line foragers (typically hermit hummingbirds) that move long distances to focal plants [39,40]. Sunbirds and honeyeaters that feed extensively on nectar-producing flowers show similar **territoriality**, but **traplining** behaviour has not been demonstrated in these groups. While the foraging behaviour of nectarivorous parrots has received surprisingly little attention in the context of pollination, lorikeets appear to forage very differently than other bird groups. Lorikeets visit large numbers of flowers per plant, such as when feeding on *Eucalyptus*, and tolerate the presence of large numbers of other lorikeets [23]. They are strong, fast-flying birds that often travel vast distances in flocks seeking out patchily distributed flowering trees [23].



Trends in Plant Science

Figure 2. Global Distribution and Diversity of the Four Major Bird Pollinator Groups. Maps were generated at a spatial resolution of 10×10 km and use the Eckert IV equal-area projection. Maps represent native, extant species only. Maps were derived by Clinton Jenkins from digital distribution maps for all the world's birds in Birdlife International and NatureServe (2013) (www.birdlife.org/datazone/info/spcdownload). (A) Honeyeaters (family Meliphagidae): ca. 180 spp., approximately half are native to Australia, many of the remainder are native to New Guinea, but some can also be found in New Zealand, remote Pacific Islands, Wallacea, and one species in Bali. (B) Sunbirds (family Nectariniidae): ca. 132 spp., with an Old World distribution that spans from Africa to Australia, across Madagascar, Egypt, Iran, Yemen, Southern China, Indian subcontinent, Indochinese peninsulas, Southeast Asia, nearby Pacific Islands, and northern Australia. Species diversity is greatest in equatorial and tropical areas. (C) Hummingbirds (family Trochilidae): ca. 340 species in two subfamilies, the hermits (subfamily Phaethornithinae) and the typical hummingbirds (subfamily Trochilinae). Species are restricted to the Americas, from South Central Alaska to Tierra del Fuego. Species richness is greatest in humid tropical and subtropical forests of the northern Andes and adjacent foothills. (D) Lorises and lorikeets (tribe Loriini within the parrot family Psittacidae): ca. 55 spp. with an Australasian distribution; they are most diverse in New Guinea, but are absent from New Zealand and arid Australia.

Aggression directed at conspecifics or other nectarivorous bird species is an important aspect of the behaviour of nectar-feeding birds, because it provides a disruption from the foraging behaviour that typically contributes to frequent self-pollination and leptokurtic pollen dispersal. For example, many Australian plant communities are dominated by large-bodied and social nectarivorous birds. These species are often highly mobile generalists and locally abundant in areas of copious nectar production [4,41], leading to frequent aggressive interactions within and among species [13]. As such, the aggressive behaviour of these nectar-feeding birds suggests greater **pollen carryover** from a wider diversity of pollen donors for the plants they pollinate compared with insects and flightless mammals, which display less aggressive behaviour.

Previous work has highlighted the effects of different functional groups of pollinators on female reproductive success, yet there has been surprisingly little empirical data exploring how different pollinator classes influence pollen-mediated gene dispersal. While the seminal review of bird pollination by Stiles [39] predicted that differences between territorial and traplining birds will have important consequences for plant mating systems and gene flow, almost four decades later there remain surprisingly few genetic tests of these predictions. The potential novel consequences of bird pollination were hinted at by rare early studies showing high outcrossing in the honeyeater-pollinated *Eucalyptus stoatei* [42], and where the hummingbird-

pollinated plant *Ipomopsis aggregata* was shown to have both high **multiple paternity** within fruits and extensive pollen carryover [43]. This finding is consistent with a recent theoretical model that predicts that the effective number of mates will be positively correlated with the extent of pollen carryover [44].

Multiple Paternity in Plants

Multiple paternity is pervasive in flowering plants [45], and occurs when the pollen from different potential sires is distributed among the flowers of a single individual, or when pollen from more than one donor is deposited on the same stigma. For a single flower, multiple paternity may arise when pollen from different donors is deposited separately during sequential visits by different pollinators, or when pollen of different donors are deposited simultaneously by a single vector carrying pollen from several plants (pollen carryover) [46]. Multiple mating promotes pollen competition, allows plants to choose among diverse male gametophytes, and can have fitness benefits through the production of more genetically variable offspring [45,47,48]. Within-fruit estimates of paternal diversity reflect pollen carryover, while estimates combining data across fruits characterise genetic diversity at the plant level. To advance our understanding of the mechanisms and consequences of paternal diversity in plants, assessments of the relative costs and benefits of multiple paternity under field conditions are required.

The incidence of multiple mating in plants can be estimated through marker-based paternity inference [45]. Such studies characterise multiple paternity directly through paternity assignment [46,49], or indirectly using coefficients of the probability of paternal identity (PPI [50]) and, from these, estimates of the effective number of sires (N_{ep}) within and among fruit (Box 1). Direct paternity assignment procedures typically include complete exclusion of nonsires or maximum likelihood procedures [51]. Despite the availability of several methodological approaches to

Box 1. Estimating the Effective Number of Sires (N_{ep})

The effective number of sires (N_{ep}), measured at the fruit or plant level, provides a fundamental parameter of ecological and evolutionary significance. As a summary parameter of paternal diversity, it allows a ready comparison among species and their biological circumstances.

Estimates of paternal diversity based on molecular marker variation use either a direct approach through paternity analysis, or an indirect approach, one of which involves the estimation of mating system parameters, such as **outcrossing rate** and correlated paternity. Direct and indirect approaches have been shown to be generally comparable [50].

The direct approach draws on accurate paternal inference to estimate the probability of paternal identity (PPI) of two offspring drawn at random from a single female, where $N_{ep} = (1/\text{PPI})$ [50,51]. In circumstances where all potential candidate sires are known, where molecular markers are sufficiently variable, and when the maternal genotype is also known, then paternity can potentially be assigned unambiguously through the total exclusion of nonsires based on Mendelian inheritance and allelic mismatches. Where this is not possible, then a paternal allocation approach can be used to choose among many candidate sires. This is the most common approach in paternity assignment studies. In categorical assignment, offspring are assigned to the candidate parent with the highest likelihood or posterior probability of being the true sire, and simulation-based methods for determining confidence in paternal assignment can be applied. Further details and other approaches are described in [49].

In the studies that used paternity assignment (Table 2, main text), we applied the approach of [51] in using r_{gg} as an unbiased measure of PPI, and the inverse of r_{gg} as the estimate of N_{ep} at the plant and population level. Here, we used Formula 3 in [51] to estimate PPI directly as a tally of the paternal matches, including selfs, from paternity assignment data supplied to us by the authors of the relevant studies.

One indirect approach draws on the correlated matings model [56] to estimate the level of correlated paternity (r_p). Correlated paternity is the degree to which seed from the same fruit or plant share the same sire, rather than are the result of a random sample of pollen from the entire population. The inverse of r_p (N_{ep}) provides an estimate of the effective number of sires. Multi-locus estimation is conducted using the software MLTR [57]. These methods have been widely used for biologically meaningful insights into plant mating [2,3,45]. Other indirect approaches include TWO-GENER and the use of relationship coefficients [51].

estimate mate diversity, in general data are surprisingly limited. Nonetheless, a few trends in relation to life-history characteristics have been deduced, including lower paternal diversity in herbs than in tree species, and for trees, higher paternal diversity for wind-pollinated than for animal-pollinated species [51,52]. However, there is a paucity of parentage studies for most pollination strategies, including vertebrate-pollinated species [53]. Thus, while multiple paternity is known to be ubiquitous, perhaps inevitable, in outcrossing terrestrial plants, a preliminary search for patterns among paternal diversity data did not reveal a specific feature that might allow us to predict the factors influencing the effective number of sires [45,53]. This is due, at least in part, to the small number of relevant studies to date, and the noise associated with confounding effects (e.g., taxonomic group, geography, or population parameters) across relatively few studies.

A Predictive Model for Pollen Movement

Although many groups of pollinators have been well studied in terms of their foraging behaviour and home ranges, a series of testable predictions related to pollen movement and mating systems in plants has yet to be developed. Based on the animal behavioural literature (see Table 1 for citations), here we predict the extent of pollen movement at varying spatial scales and the likely contributing processes for different groups of pollinators (Table 1, and references therein). We have undertaken this at two levels; between the major behavioural types in specialist nectar-feeding birds (territorial birds, trap-lining hummingbirds, and lorikeets) and between bird pollination and other systems (bees, bats, moths, and nonflying mammals) common in genera that contain bird-pollinated plants.

We predict that pollen dispersal within and among stands is likely to be more extensive for plants pollinated by traplining birds than for plants pollinated by territorial birds. There is evidence that plants pollinated by traplining hermit hummingbirds are more likely to be self-compatible than those pollinated by nonhermits and other pollinators, suggesting that traplining behaviour ameliorates the risks of pollinator-mediated selfing in these self-compatible species [38]. For plants pollinated by territorial birds, the extent of pollen-mediated gene dispersal will also depend on the magnitude of aggressive interactions by avian visitors to focal plants. These aggressive interactions can be either interspecific or intraspecific and are affected by the amount of nectar available relative to bird density. For example, aggressive interactions may increase in frequency in larger plant populations with greater nectar crops that support high numbers of behaviourally dominant bird species [13]. Lorikeets show a different pattern of foraging, where they forage on large numbers of flowers per plant, but can move long distances in search of nectar sources, suggesting not only high levels of within plant pollen transfer, but also the potential for long-distance dispersal [19].

Bats, nonflying mammals, and, in some cases, bees also engage in aggression during nectar feeding, but are less likely to generate significant disturbances to foraging behaviour, suggesting that bird pollination leads to comparatively greater pollen dispersal within stands of flowering plants. However, similar to territorial birds, bees and flightless mammals involved in pollination generally move within a home range of less than 5 ha, which establishes a predicted upper limit for most pollen movement. Alternatively, traplining hummingbirds move considerable distances, and bats and lorikeets have large home ranges that can lead to pollen movement between distant stands. At the landscape scale, with the exception of bees and flightless mammals, some members of all groups undertake regional movements, either being nomadic, migratory, or undertaking regular movements to distant food resources. As such, we predict that most of these groups of pollinators have a capacity to effect some level of long-distance pollen dispersal.

Given that the transition from bee to bird pollination (not including parrots) is perhaps the most common evolutionary pathway to bird pollination [17,18], it is worth focussing in more detail on

Table 1. Predictive Model for Pollen Movement based on Behaviour of Territorial Birds, Traplining Birds, Hummingbirds, Lorikeets, Bees, Moths, Flightless Mammals, and Bats^a


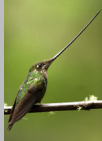



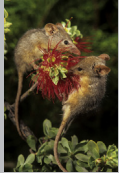


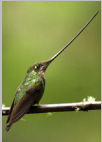


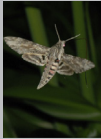
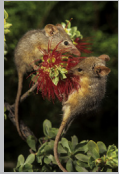

	(1) 	(2) 	(3) 	(4) 	(5) 	(6) 	(7) 
Functional group	Territorial bird	Traplining bird	Lorikeet parrots	Bee	Lepidoptera (moths and butterflies)	Flightless mammal	Bat
Examples	Honeyeaters, hummingbirds, sunbirds	Hermit hummingbirds, sword-billed hummingbird	Australian lorikeets	Honeybees, bumblebees, numerous solitary bees	Hawkmoths	Possums, rodents	Blossom bats
Contributing Processes							
Pollen carryover	High, flatter curve than insects [90]	High, indirect evidence, more than territorial [91]	Not studied	Moderate, steeper curve than birds [16], reduced by grooming [92,93]	Not studied	Low, steep curve due to frequent grooming [94]	High, less-steep curve than birds [90]
Foraging strategy	Forages within nectar-rich stand, moves to near-neighbour plants [13,95]	Moves to relatively small, dispersed resources [13]	Numerous flowers per plant, can move to dispersed resources [23,96]	Move to near-neighbours of preferred plants [11]	Move to near-neighbours of preferred plants [97,98]	Not studied	Moves to dispersed resources [99,100]
Home range impacts on axial variance	Moderate, typically <3 ha, <1 ha [23,101,102]	High, can move >1 km from lek [95,103]	High	Small bees <3 ha, larger bees up to 700 ha [104–107]	Unknown	0.1–300 ha, typically <5 ha [82,108–110]	High; 12–1800 ha [99,111–113]
Long-distance movements (>5 km)	Some species, seasonal movements, nomads, and migrants [27,40]	Some species, seasonal movements, nomads, and migrants [40]	High, follow patchy nectar resources	No, some exceptions (e.g., <i>Apis</i> , euglossine bees) [93,114]	Rarely, but possible in migrants [115–117]	Low	High, forage over broad areas from roost
[111,117,118]							
Aggression	High, disrupts foraging [13,27,101,119]	Moderate [95,101]	Moderate, but not usually sufficient to greatly disrupt foraging [23,96]	Rarely [120–122]	Absent	Rarely [123]	Moderate, in some species, disrupts foraging [100]

Table 1. (continued)

	(1) 	(2) 	(3) 	(4) 	(5) 	(6) 	(7) 
Predicted Pollen Movement							
Relative frequency of within versus among plant movements	Moderate	Low	High	Moderate-high	Low-high	High	High
Distance within stands	Moderate	High	Moderate	Low-moderate (euglossine bees likely an exception)	Low-moderate	Low	Moderate
Between stands (>500 m)	Some cases yes, dispersed resources, outside of breeding season	Yes	Yes	No, some exceptions (e.g., <i>Bombus</i> , <i>Apis</i> , euglossine bees)	Typically no, occasional longer movements	No	Yes
Long distance dispersal via migrants, nomads, seasonal movement (>5 km)	Yes	Yes	Yes	No, some exceptions (e.g., <i>Apis</i> , euglossine bees)	Yes	No	Yes

^aSpecies shown in photos: (1) eastern spinebill (*Acanthorhynchus tenuirostris*) (Benjamin Twist); (2) sword-billed hummingbird (*Ensifera ensifera*) (Herbert Stärker); (3) rainbow lorikeet (*Trichoglossus haematodus*) (Fir0002/Flagstaffotos); (4) African honeybee (*Apis mellifera scutellata*) (Steve Johnson); (5) convolvulus hawkmoth (*Agrius convolvuli*) (Steve Johnson); (6) honey possum (*Tarsipes rostratus*) (Jiri Lochman); (7) lesser long-nosed bat (*Leptonycteris curasoae*) (www.merlintonuttle.org).

the difference between these two pollinator functional groups. At small spatial scales, bees are likely to have comparatively more frequent within-plant movements and shorter pollen distance dispersal due to a combination of optimal foraging behaviour, comparatively short flight distances, and regular **pollen grooming** leading to less pollen carryover. Although there are known movements of at least 6 km in the bee genera *Apis* and *Bombus* and the tribes Euglosini and Xylocopini, most bees and most nectarivorous territorial birds have home ranges of less than 3 ha. However, in territorial birds, because of pollen carryover and frequent interruptions to foraging behaviour through aggression, we predict that, despite similar home ranges to most bees, birds will more frequently disperse pollen from a larger number of individuals more widely within stands. At larger scales, birds that undertake seasonal or dispersive movements in pursuit of patchy nectar resources are more capable of mediating pollen dispersal distances of many kilometres.

Consequences of Bird Pollination for Plant Mating: Testing the Predictions

Detailed mating studies for bird-pollinated plants are in their infancy. For example, in a recent review [54], only five of 92 paternity studies of trees were species that included birds as pollinators, demonstrating an overwhelming focus to date on insect and/or wind pollination systems from the Northern Hemisphere. However, recent studies on plants that include honeyeaters as pollinators revealed high levels of multiple mating and a significant departure from near-neighbour mating that typifies plants pollinated by insects (Table 2). Drawing on the global literature, we reviewed 16 studies that have applied genetic markers to measure multiple paternity (N_{ep} , the mean effective number of sires per plant) for plants pollinated by birds, and contrasted to an equivalent number of plant species pollinated by insects. Multiple paternity was estimated either from paternity assignment data using the method of [50] or from the inverse of the estimate of correlated paternity (r_p) as calculated in MLTR [55,56] (Box 1). The mean effective number of sires per plant for bird-pollinated plants ($N_{ep} = 12.37$; $N = 16$) was significantly greater ($F_{1,32} = 7.37$, $P = 0.012$) and almost twice that of plants pollinated solely by insects ($N_{ep} = 6.86$; $N = 18$).

From this summary, we draw four main conclusions: (i) there is evidence of higher paternal diversity for plants that include birds as pollinators compared with those pollinated only by insects; (ii) there are clear exceptions to this general conclusion, with very low N_{ep} for some bird-pollinated plants and very high N_{ep} for some insect-pollinated plants; (iii) almost all bird-pollinated plants studied were also visited by insects and mammals, thus obscuring the influence of bird pollinators alone; and (iv) there are few mating system studies of bird-pollinated plants outside of Australia. Based on pollinator behaviour, we suggest that insect and/or flightless mammal contributions to pollination are likely to reduce the paternal diversity through lower mobility and/or lower pollen carryover than that associated with bird pollination alone. To tease apart these contributions to pollination, while avoiding the potentially confounding factors associated with variation in plant and population properties that impact paternal diversity, ideally requires pollinator exclusion experiments on plants pollinated by all three pollinator groups (see Concluding Remarks below). Nonetheless, these data suggest that bird pollination is a strong predictor of multiple paternity in plants, with significant evolutionary and conservation consequences.

Mating Systems and the Evolutionary Consequences of Bird Pollination

This new insight into multiple mating in these plants has important implications for understanding the evolutionary consequences of bird pollination [19]. Multiple mating is of evolutionary significance because it impacts the genetic diversity and relatedness among maternal sibs within and among fruits, and, hence, initially the response to selection when competing for maternal resources during seed maturation. Under limited seed dispersal, multiple mating may lessen the intensity of competition among siblings, potentially increasing maternal fitness

Table 2. Estimates of Mean Effective Number of Sires per Plant (N_{ep})^a for Plants Pollinated by Birds or Insects

Species	Family	Pollinator ^b	N_{ep}	P/M	Location	Self-Incompatible?	Habit	Refs
Plants Pollinated by Birds								
<i>Banksia hookeriana</i>	Proteaceae	Bird/insect/mammal	26.5	P	Western Australia	Y	Small tree	[124]
<i>Eucalyptus caesia</i>	Myrtaceae	Bird/insect/mammal	24	P	Western Australia	N	Tree	[125]
<i>Eucalyptus globulus</i>	Myrtaceae	Bird/insect/mammal	22.2	M	Eastern Australia	N	Tree	[126]
<i>Banksia attenuata</i>	Proteaceae	Bird/insect/mammal	17.3	P	Western Australia	Y	Small tree	R. Omodei, Honours thesis, University of Western Australia, 2008
<i>Ipomopsis aggregata</i>	Polemoniaceae	Bird	17.1	M	North America	Y	Small shrub	[43]
<i>Banksia oligantha</i>	Proteaceae	Bird/insect/mammal	12.5	M	Western Australia	N	Small tree	[2]
<i>Calothamnus quadrifidus</i>	Proteaceae	Bird/insect/mammal	12.2	M	Western Australia	N	Shrub	[2]
<i>Banksia ilicifolia</i>	Proteaceae	Bird/insect/mammal	11.7	P	Western Australia	N	Tree	D. Roberts et al., unpublished
<i>Eucalyptus ramelliana</i>	Myrtaceae	Bird/insect/mammal	11.1	M	Western Australia	N	Tree	[2]
<i>Eucalyptus gracilis</i>	Myrtaceae	Bird/insect/mammal	10.3	M	South Australia	N	Tree	[74]
<i>Lambertia orbifolia</i>	Proteaceae	Bird	8.5	M	Western Australia	N	Small tree	[2]
<i>Banksia cuneata</i>	Proteaceae	Bird/insect/mammal	8.3	M	Western Australia	N	Small tree	[127]
<i>Eucalyptus incrassata</i>	Myrtaceae	Bird/insect/mammal	5.9	M	South Australia	N	Tree	[128]
<i>Banksia sphaerocarpa</i>	Proteaceae	Bird/insect/mammal	4.8	P	Western Australia	N	Small tree	[129]
<i>Calothamnus quadrifidus</i>	Myrtaceae	Bird/insect/mammal	3.2	M	Western Australia	N	Shrub	[130]
<i>Grevillea iaspicula</i>	Proteaceae	Bird/insect	2.4	M	Eastern Australia	N	Shrub	[131]
Plants Pollinated by Insects								
<i>Echinacea angustifolia</i>	Asteraceae	Bee/butterfly/beetle	23.3	P	North America	Y	Herb	[132]
<i>Arabidopsis halleri</i>	Brassicaceae	Insect	21	M	Europe	Y	Herb	[133]
<i>Acacia anfractuosa</i>	Mimosaceae	Insect	10	M	Western Australia	N	Small tree	[2]
<i>Centaurea solstitialis</i>	Asteraceae	Insect	8.8	M	Europe	N	Herb	[134]
<i>Sorbus torminalis</i>	Rosaceae	Insect	7.1	M	Europe	N	Tree	[135]
<i>Centaurea corymbosa</i>	Asteraceae	Insect	5.1	M	Europe	Y	Herb	[52]
<i>Daviesia mimosoides</i>	Fabaceae	Bee	5	M	Eastern Australia	N	Shrub	[136]
<i>Verticordia fimbrialepis</i>	Myrtaceae	Insect	4.8	M	Western Australia	N	Shrub	[137]
<i>Eurycorymbus cavaleriei</i>	Sapindaceae	Insect	4.8	M	Asia	Dioecious	Tree	[138]
<i>Mimulus guttatus</i>	Phrymaceae	Bee	4.7	M	North America	N	Shrub	[56]
<i>Eichornia paniculata</i>	Pontederiaceae	Bee	4.2	M	South America	Dioecious	Aquatic herb	[139]
<i>Acacia sciophones</i>	Mimosaceae	Insect	4	M	Western Australia	N	Small tree	[2]
<i>Daviesia suaveolens</i>	Fabaceae	Bee	4	M	Eastern Australia	N	Shrub	[136]
<i>Eucalyptus pauciflora</i>	Myrtaceae	Insect/bird/mammal	5	M	Eastern Australia	N	Tree	[140]
<i>Mimulus ringens</i>	Phrymaceae	Bee	4	M	North America	N	Herb	[44]
<i>Persoonia mollis</i>	Proteaceae	Bee	3.1	P	Eastern Australia	N	Small tree	[141]
<i>Albizia julibrissin</i>	Fabaceae	Insect	2.9	M	Asia	Y	Tree	[142]
<i>Glycine argyrea</i>	Fabaceae	Insect	1.8	M	Eastern Australia	N	Small shrub	[143]

^a N_{ep} measured by paternity (P) or MLTR (M); see Box 1 (main text) for explanation.^b'Bird/mammal/insect' indicates birds are the main visitors and likely to be the most effective pollinators.

through greater numbers of genetically diverse offspring [57]. While increased seedling survival was associated with multiple paternity in *Eucalyptus gracilis* [47], experimental evidence is needed from other systems to test the hypothesis that multiple paternity increases offspring fitness via genetic gains.

The advantage of increased pollen dispersal and higher multiple paternity from bird versus insect visitors is compatible with the idea that some floral traits often seen as adaptations to bird pollination, may in fact be mechanisms to reduce insect visitation. For example, while red floral colouration is readily detectable by birds [58], it is less readily detected by nectar-foraging hymenoptera than are shorter wavelengths of light [59]. Furthermore, floral traits, such as long floral tubes, which increase the efficiency of birds at removing and depositing pollen, may also have a secondary role in minimising visits by less-effective insect pollinators [19]. Similarly, the nectar of some bird-pollinated plants has been shown to be distasteful to insects [60], and the typically low sugar concentration of bird-pollinated plants may be comparatively suboptimal for bees [19], thereby acting as a deterrent [61].

The evolution of traits associated with bird pollination may also have important consequences for ongoing floral evolution. For example, bird-pollinated flowers acted as a preadaptation to the evolution of hawkmoth pollination in *Aquilegia* following an increase in nectar spur length [62]. In some systems, bird pollination constrains the evolutionary potential for future switches in pollination strategy, such as through the loss of the ability to produce pigments needed to attract bees [63]. Furthermore, loss of particular components of the floral odour involved in pollinator attraction may limit potential pollinator shifts. The ecology of nectarivorous birds could also affect rates of speciation and extinction in the plants that they pollinate. Recent phylogenetic research in some genera of Australian Fabaceae showed that bird-pollinated lineages are on average less diverse than bee-pollinated lineages [17]. Similarly, comparative phylogenetic research suggests that, once hummingbird pollination evolves within clades with bee pollination, further speciation is rare [18]. Based on these findings, it has been hypothesised that extensive long-distance movement of pollen by birds reduces allopatric speciation and diversification rates, and bird pollination *per se* may not be a diversifying factor.

Conservation and Restoration Consequences of Bird Pollination

Pollinator decline in anthropogenically modified landscapes has been identified as a global threat to ecosystem services in wild plant populations, impacting thousands of plant species [64–66]. For example, markedly reduced fruit set leading to population decline was associated with the loss of avian pollinators in New Zealand [67]. Increasingly, reinstating pollinator services is recognised as critical for the self-sustainability of restored plant communities [68–70]. Furthermore, for threatened species recovery programs, reintroductions of plants with ecologically specialised pollination systems are usually unsuccessful in the longer term unless the distribution and habitat preference of the pollinator is incorporated into the management plan before plant reintroduction [71].

While the primary focus of the literature relating to declining pollinator populations has been on demographic issues for plants, genetic consequences are also important. Lower multiple paternity can have negative conservation consequences for conservation through reduced heterozygosity, genetically effective population size [48], and fitness [58]. In some regions, invasive pollinator species, such as honeybees and bumblebees, are having a major impact on many bird-pollinated plants by reducing fecundity, outcrossing, and mate diversity [72]. Alternatively, the high mobility of many nectarivorous birds suggests that the impact of disturbance and fragmentation to plant mating patterns can be mitigated through frequent pollinator-mediated gene flow [73–75]. For example, polyandry increased with increasing geographical isolation of isolated paddock trees for the primarily bird-pollinated *Eucalyptus*

leucoxylon, but not for the primarily insect pollinated *Eucalyptus camaldulensis* [76]. Similarly, highly mobile bird pollinators can rapidly restore genetic connectivity and pollinator services in rehabilitated plant communities, a critical requirement for self-sustainability [68,70,77]. However, in Australia, the increased prevalence of highly aggressive ‘competitive despot’ bird species (e.g., the noisy miner *Manorina melanocephala*) in fragmented remnant vegetation is excluding smaller species, with potentially detrimental impacts on pollination, seed set, and plant persistence [78]. From the perspective of the plant, it remains to be established whether these dominant birds are as effective pollinators as the original honeyeater community.

Concluding Remarks and Future Perspectives

We advocate testing our predictions by combining cutting-edge molecular analyses of paternity with elegant field experiments that quantify siring success by different classes of pollinator on the same plant species. This approach avoids potentially confounding effects of phylogeny, floral traits, and differences in ecology when making comparisons across species. Similarly, experimental manipulation of plant population size and density will be critical in testing the prediction that bird pollinators can ameliorate the genetic effects of small population size. An important component in both of these avenues of investigation will be to combine estimates of pollen dispersal distances with fitness estimates (e.g., fecundity, seed viability, and offspring vigour) to formally test the consequences of different patterns of pollen dispersal.

Genotyping of individual pollen grains recovered from pollinators will allow powerful tests of pollen carryover. For example, paternity analyses based on microsatellite genotyping of individual pollen grains found on insect pollinators (bees, flies, and beetles) visiting Japanese chestnut (*Castanea crenata*) trees showed that all insect groups carried outcross pollen grains for long distances via pollen carryover, suggesting that a wide range of insects are potential outcross-pollen vectors for this **self-incompatible** species [79]. This study also highlights that, in plants visited by a diverse assemblage of pollinators, single pollen grain genotyping will make it possible to readily compare the extent of pollen carryover by different pollinator species. Recent developments in the use of next generation sequencing for DNA metabarcoding of pollen [80,81] provide new opportunities to assess pollen carryover. While currently limited to species-level identification, the potential exists to extend these methods to genetic diversity in mixed-pollen samples from pollinators, or even individual identification.

One of the major challenges in understanding how different pollinator groups influence mating patterns is determining the underlying behavioural mechanisms responsible for pollen movement. In particular, among territorial birds there can be pronounced seasonal, population-level, and interspecific variation in foraging behaviour and the extent of aggression [82]. Traditional methods, such as direct observation of colour-banded individuals, are useful for determining home ranges and recognising behaviourally dominant individuals. These can be complemented by ethological experimentation and the tracking of animals for detailed analysis of foraging behaviour, particularly for more cryptic species, and enable the detection of rarer long-distance movements that are likely to be critical for plant gene flow. For example, radiotelemetry studies have demonstrated that pollinators move longer distances than expected based on direct observation and, in many cases, are likely to have the capacity to link spatially segregated plant populations [83]. While the tracking of animals has previously been limited to large-bodied species, recent technological advances on two levels will generate unprecedented insight into the movements of all vertebrate pollinators and even large insects [84,85]. Reductions in transmitter size, primarily through advances in the technology of batteries, mean that almost all nectarivorous vertebrates, and even larger-bodied insects, can now be tracked [86]. Furthermore, transmitters with GPS are accurate and allow constant recording of the location of the animal, without a human observer [85]. Radiotransmitters with GPS are not yet small enough for most pollinators but soon will be [85]. Harmonic radar and RFID are potentially powerful

Outstanding Questions

Is multiple paternity within fruits influenced primarily by pollen carryover in single pollinator visits or by sequential visits to a flower?

Does a decline or loss of avian pollinators impact the fitness of plants adapted for bird pollination, and how much do insects contribute to the pollination of bird-adapted flowers?

Are frequent nectarivores more or less effective at cross-pollination than occasional nectarivores?

How do behavioural differences associated with different groups of birds influence paternal diversity in the plants they pollinate?

techniques with minute transmitters, but their cost and restriction to a small spatial range have limited their use.

Increasingly sophisticated heat- and movement-triggered motion-sensor cameras (e.g., see Video S1 in the supplementary information online) with a capacity for filming use infrared illumination is an exciting recent technological development for pollination biology studies [87,88]. This technology offers opportunities for new insight into the natural behaviour of bird pollinators and consequences for the plants that they visit. This technology can aid in quantifying visitation rates to individual flowers and inflorescences, and enable continuous monitoring 24 h/day to dramatically increase both the total observation time, and the detection of rare and/or night-time visits. For example, motion-triggered camera footage was used to confirm that the critically endangered orchid *Satyrium rhodanthum* was pollinated solely by a single species of sunbird, despite the presence of other potential pollinators [89]. Furthermore, deploying numerous cameras for concurrent observations with a precise and coordinated recording of time and duration of visitation enables the accurate tracking of pollinator movements within and among plants.

Integrating the use of these new technologies with traditional field-based observations will allow unprecedented insight into the foraging behaviour of birds and the testing of predictions for pollen movement and plant mating (see Outstanding Questions). Given the taxonomic and behavioural diversity of avian pollinators, and the diversity of plants involved, much remains to be learned about bird pollination and its evolutionary ecological consequences for plant mating.

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Supplemental Information

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