SPECIAL PAPER

Nectar-feeding bird and bat niches in two worlds: pantropical comparisons of vertebrate pollination systems

Theodore H. Fleming* and Nathan Muchhala

Department of Biology, University of Miami, Coral Gables, FL 33124, USA

ABSTRACT

Aim We review several aspects of the structure of regional and local assemblages of nectar-feeding birds and bats and their relationships with food plants to determine the extent to which evolutionary convergence has or has not occurred in the New and Old World tropics.

Location Our review is pantropical in extent and also includes the subtropics of South Africa and eastern Australia. Within the tropics, it deals mostly with lowland forest habitats.

Methods An extensive literature review was conducted to compile data bases on the regional and local species richness of nectar-feeding birds and bats, pollinator sizes, morphology, and diets. Coefficients of variation (CVs) were used to quantify the morphospace occupied by the various families of pollinators. The extent to which plants have become evolutionarily specialized for vertebrate pollination was explored using several criteria: number and diversity of growth forms of plant families providing food for all the considered pollinator families; the most common flower morphologies visited by all the considered pollinator families; and the number of plant families that contain genera with both bird- and bat-specialized species.

Results Vertebrate pollinator assemblages in the New World tropics differ from those in the Old World in terms of their greater species richness, the greater morphological diversity of their most specialized taxa, and the greater degree of taxonomic and ecological diversity and morphological specialization of their food plants. Within the Old World tropics, Africa contains more specialized nectar-feeding birds than Asia and Australasia; Old World nectar-feeding bats are everywhere less specialized than their New World counterparts.

Main conclusions We propose that two factors – phylogenetic history and spatio-temporal predictability (STP) of flower resources – largely account for hemispheric and regional differences in the structure of vertebrate pollinator assemblages. Greater resource diversity and resource STP in the New World have favoured the radiation of small, hovering nectar-feeding birds and bats into a variety of relatively specialized feeding niches. In contrast, reduced resource diversity and STP in aseasonal parts of Asia as well as in Australasia have favoured the evolution of larger, non-hovering birds and bats with relatively generalized feeding niches. Tropical Africa more closely resembles the Neotropics than Southeast Asia and Australasia in terms of resource STP and in the niche structure of its nectar-feeding birds but not its flower-visiting bats.

*Correspondence: Theodore H. Fleming, Department of Biology, University of Miami, Coral Gables, FL 33124, USA.
E-mail: tfleming@fig.cox.miami.edu

INTRODUCTION

It has long been known that most tropical plants rely on animals for pollination (Regal, 1982; Bawa, 1990; Pellmyr, 2002). In tropical rain forests, up to 98–99% of species are animal-pollinated; a lower percentage of species (typically *c.* 70% in trees and *c.* 20% in vines) are animal-pollinated in tropical dry forests (Bawa, 1990; Bullock, 1995). The vast majority of animal-pollinated plants rely on insects, particularly on a wide range of bees, for pollination. Relatively few plants (typically 3–11% per habitat; Devy & Davidar, 2003) are pollinated by birds or mammals. Nonetheless, this represents a substantial number of tropical plants of various growth habits (trees, shrubs, herbs, epiphytes, and vines; Fleming *et al.*, 2005). For example, in the lowland tropical rain forest at La Selva, Costa Rica, about 25% of understorey plant species are vertebrate-pollinated ($n = 151$ species); these percentages are about 12% and 8% for subcanopy ($n = 74$) and canopy ($n = 51$) trees, respectively (Kress & Beach, 1994). Out of approximately 13,500 genera of tropical plants, birds are thought to pollinate species in about 500 genera, and bats those in about 250 genera (Sekercioglu, 2006).

A substantial adaptive radiation of tropical and subtropical flower-visiting and nectar-feeding birds and bats has occurred in association with the pollination of these flowers. This radiation has taken place independently in the Old and New World tropics, and, as we discuss in this paper, details of these radiations differ strikingly between the hemispheres. These details include differences in: (1) taxonomic richness at regional and local scales; (2) body masses and hovering ability; and (3) degree of feeding specialization, resulting from different degrees of evolutionary specialization for vertebrate pollination by tropical plants. In addition to documenting inter-hemispheric differences, our objective here is to determine the extent to which tropical forests in different biogeographical regions have converged in the structure and function of their vertebrate pollination systems. Are vertebrate nectar-feeding niches the same in the Old and New World tropics? As Primack & Corlett (2005) emphasize, despite sharing many physiognomic features, tropical forests around the world differ markedly in many features as a result of different geological and evolutionary histories. The dominance of mast-flowering and mast-fruiting trees of the Dipterocarpaceae in the aseasonal lowland Asian tropics, for example, has had a profound effect on flowering and fruiting phenology and on the ecology and evolution of nectar- and fruit-eating vertebrates (Fleming *et al.*, 1987; Corlett, 1998, 2004; Curran & Leighton, 2000; Sakai, 2001). Thus, we initially expected to see biogeographical differences in vertebrate pollination systems. However, the details of these differences are worth exploring in order to understand the ecological and historical limits to adaptive radiations and evolutionary convergence.

Our initial hypothesis in this paper is that New World nectar-feeding vertebrates have evolved a greater number of, and more specialized, interactions with their food plants than their Old World counterparts. This hypothesis reflects, in part, the fact that Neotropical hummingbirds are usually considered to be the most specialized avian nectar-feeders in the world (Stiles, 1981; Schuchmann, 1999; Cheke & Mann, 2001; Nicolson & Fleming, 2003). It also reflects the fact that the Neotropical angiosperm flora is the richest in the world in terms of taxonomic and ecological diversity (Gentry, 1982; Whitmore, 1998). If this hypothesis is true, we might expect to find a greater number of evolutionary origins and higher species richness in nectar-feeding vertebrates and their food plants, including the use of birds and bats as pollinators by a greater variety of plant growth forms, in the New World than in the Old World. In addition to their higher species richness, we expect to see a greater diversity of floral and pollinator morphologies and a finer partitioning of pollinator species by plants in the Neotropics. The results of our analyses generally support this hypothesis, but they also indicate that the extent of evolutionary specialization on vertebrate pollinators varies significantly within the Old World tropics. It appears to be significantly greater in Africa than in Southeast Asia and Australasia. Thus, in reality, our 'two worlds' perspective based on a New World vs. Old World dichotomy is too broad. There are at least three tropical worlds from the perspective of nectar-feeding vertebrates and their food plants – the Neotropics; Africa and seasonal parts of Asia; and aseasonal Southeast Asia and Australasia.

ECOLOGICAL VS. EVOLUTIONARY SPECIALIZATION

Before we examine our initial hypothesis and its predictions in detail, we need to define what we mean by 'specialization' and how we might distinguish between 'specialized' and 'generalized' pollination systems. These terms have been widely discussed in the recent literature (e.g. Waser *et al.*, 1996; Armbruster *et al.*, 2000; Johnson & Steiner, 2000; Fenster *et al.*, 2004; Armbruster, 2006; Ollerton *et al.*, 2006, 2007), and several types of specialization need to be distinguished. *Ecological specialization* is defined in terms of the specificity of the interaction; for example, an ecologically generalized plant uses many species of pollinators whereas an ecologically specialized plant uses few species. For plant–pollinator interactions, however, the absolute number of interacting species is less important than the number of types of interactors, in terms of their taxonomic/functional affinities (Fenster *et al.*, 2004). For example, a plant pollinated by 10 moth species could be considered more ecologically specialized than another plant pollinated by five insect species from five different orders (Johnson & Steiner, 2000). Therefore in this paper we use ecological specialization with reference to the number of functional groups involved in the interaction. From a plant's perspective, an ecologically generalized flower is pollinated by bats, birds, and bees (regardless of the number of species) and an ecologically specialized flower is pollinated only by bats. From an animal's perspective, an ecologically generalized pollinator consumes fruit and insects as well as nectar/pollen, while an

ecologically specialized pollinator is dedicated completely (or nearly so) to a diet of nectar/pollen.

Phenotypic specialization refers to traits that adapt an organism to its mutualistic partner. From an animal's perspective, this can include adaptations to aid in the detection of flowers or the extraction of nectar; for example, the highly extendable tongue of glossophagine nectar bats represents a phenotypic specialization to aid in feeding on flowers with long corollas. From a plant's perspective, phenotypic specialization could include floral traits that increase rewards or attractants or that improve the morphological fit with a particular type of pollinator (Wilson *et al.*, 2006). Phenotypic specialization often correlates with ecological specialization, but not necessarily. For example, Aigner (2001) pointed out that a flower pollinated primarily by hummingbirds may evolve phenotypic specializations to bees as long as this does not reduce the effectiveness of hummingbirds; in this case, phenotypic specialization leads to ecological generalization (i.e. to an increase in the number of types of pollinators).

Evolutionary specialization refers to the process of evolving towards increased *ecological specialization* (e.g. specificity) (Armbruster *et al.*, 2000). From a plant's perspective, increased specificity is achieved through the evolution of a combination of *phenotypic specializations* that increase the effectiveness of the primary pollinator and, more importantly, that restrict access by other floral visitors. For example, long corolla tubes in many hummingbird flowers restrict access by nectar-collecting bees and represent an evolutionary specialization in comparison with short-tubed ancestral species. The well-known pollination syndromes (Faegri & van der Pijl, 1979; Proctor *et al.*, 1996) reflect this evolutionary specialization. In this paper, we focus on issues dealing with evolutionary specialization, which can result in ecological and phenotypic specialization.

PATTERNS OF TAXONOMIC RICHNESS

The major families of tropical vertebrate nectar-feeders are listed in Table 1. Except where noted, our avian taxonomy follows Sibley & Monroe (1990), and our mammalian taxonomy follows Simmons (2005). Although many other vertebrates occasionally visit flowers, in this paper we will focus on those families containing nectar specialists, that is, families with species for which nectar (and sometimes pollen) comprises > 50% of their diets. In the New World, hummingbirds are the major avian pollinators and have undergone a spectacular radiation that began in the early Cenozoic. Recent fossil evidence suggests that early hummingbird evolution is likely to have taken place in the Oligocene in the Old World (Mayr, 2004, 2005, 2007). By the early Miocene (about 17 Ma), which is when the major radiation of present-day New World taxa began (Bleiweiss, 1998a,b), hummingbirds were extinct in the Old World. The family currently contains about 330 species in 102 genera in two ecologically distinct subfamilies, namely the hermits (Phaethornithinae) with six genera and 34 species, and 'typical' hummingbirds (Trochilinae) with 96 genera and 294 species (Schuchmann, 1999). The general ecology of these birds is reviewed in Stiles (1981, 2004), Schuchmann (1999) and Fleming *et al.* (2005). Based on our criteria above, hummingbirds are not completely ecologically specialized to nectar because many species also eat insects. Compared with other nectar-feeding birds, however, they are highly specialized for a nectarivorous life. Other New World nectar-feeders include a variety of passerines, including

Table 1 The major families of nectar-feeding birds and mammals in tropical forests.

Hemisphere	Taxon	Family (no. genera, no. species)	Regional distribution	No. genera, no. species
New World	Birds	Trochilidae – hummingbirds	Throughout the Neotropics	106, 328
	Bats	Phyllostomidae (part) – Glossophaginaes	Throughout the Neotropics	16, 38
Old World	Birds	Psittacidae (part) – lorikeets (12, 53)	Asia only	4, 13
			Asia + Australasia	8, 40
		Nectariniidae (part) – sunbirds (16, 130)	Africa	11, 88
			Asia only	7, 40
			Asia + Australasia	2, 2
		Nectariniidae (part) – flowerpeckers (2,44)	Asia	2, 37
			Australasia	1, 7
		Meliphagidae – honeyeaters (42, 176)	Asia	5, 21
			Australasia	38, 155
		Zosteropidae – whiteeyes (13, 95)	Africa	2, 19
			Asia	8, 38
			Australasia	5, 38
	Bats	Pteropodidae (part) – 'macroglossines' (6, 15)	Africa	1, 1
			Asia only	3, 7
			Asia + Australasia	1, 1
			Australasia	3, 6

Not all of the species tallied here are necessarily forest-dwellers, but the bulk of them are. Sources of data: Sibley & Monroe (1990), Schuchmann (1999), Cheke & Mann (2001) and Simmons (2005).

bananaquits (Emberizidae, Coeribini), orioles (Emberizidae, Icterini), and, seasonally, paruline warblers (Emberizidae, Parulini) (Stiles, 1981).

Mammalian counterparts of hummingbirds are glossophagine bats (von Helversen, 1993; von Helversen & Winter, 2003), a clade of New World leaf-nosed bats (Phyllostomidae) containing about 38 species classified in 16 genera (Simmons, 2005). Based on molecular and fossil evidence, the Phyllostomidae is about 39 million years old (Jones et al., 2005; Teeling et al., 2005), and Davalos (2004) has estimated that glossophagine bats are at least 12 million years old. Bats of the genus Phyllostomus and certain mostly frugivorous phyllostomids (e.g. Carollia, Artibeus) also visit flowers opportunistically (e.g. Heithaus et al., 1974, 1975; Sazima & Sazima, 1975; Sazima et al., 1999), as do several non-volant Neotropical mammals including a few opossums, rodents, and monkeys (e.g. Janson et al., 1981; Ferrari & Strier 1992; Tschapka & von Helversen, 1999). However, since these mammals are not nectar specialists, in this study we focus mainly on glossophagines.

The Old World ecological counterparts of hummingbirds and glossophagine bats include several families of birds and nectar-feeding bats of the Pteropodidae (flying foxes and their relatives) (Table 1). The closest ecological analogues of hummingbirds are sunbirds (Nectariniidae, Nectariniini), a clade of passerines containing 16 genera and about 130 species (Cheke & Mann, 2001). According to the phylogeny of Barker et al. (2004), sunbirds and their relatives (the flower peckers, Nectariniidae, Dicaeini) are advanced members of the 'Passerida', whose radiation began in the Oligocene or Miocene (i.e. 30–20 Ma). With 11 genera and 88 species, Africa contains more sunbirds than Asia (7 genera and 40 species); two species are Australasian. The largest and oldest group of Old World nectar-feeding birds is the honeyeaters (Melaphagidae), whose distribution is mostly Australasian (Table 1). This passerine family contains about 42 genera and 176 species (Sibley & Monroe, 1990) and is likely to date from the Eocene (c. 50–45 Ma) (Barker et al., 2004). Less diverse Old World families or subfamilies of avian nectarivores include two groups of passerines – the flowerpeckers, which are strongly associated with the flowers and fruits of mistletoes (Loranthaceae), and white-eyes (Zosteropidae) – and brush-tongued parrots (Table 1). Flowerpeckers are more diverse in tropical Asia than in Australasia, whereas white-eyes occur in Africa, Asia and Australasia, and are equally diverse in the latter two regions. Lories are mostly Australasian in distribution. Like honeyeaters, they are a relatively old group, probably dating from the early Cenozoic (Forshaw, 2006).

Most of the Old World mammalian nectar-feeders are bats of the family Pteropodidae. Classified in a different suborder (Yinpterochiroptera) from phyllostomid bats (Yangochiroptera), this family is about 56 Myr old, although its crown group (i.e. extant species) dates from about 25–28 Ma (Jones et al., 2005; Teeling et al., 2005). Six genera containing only 15 species have traditionally been viewed as 'dedicated' nectar-feeders based on skull morphology (e.g. Freeman, 1995), but

recent molecular and morphological studies indicate that these so-called 'macroglossines' are paraphyletic (Kirsch et al., 1995; Giannini & Simmons, 2005). All but one of these genera and species occur in Asia or Australasia; Megaloglossus minimus represents an independent, relatively recent evolution of nectar-bat morphology in Africa (Giannini & Simmons, 2005). Many other pteropodids, including members of the large genus Pteropus (c. 65 species), are well-known flower-visitors (e.g. Baker & Harris, 1957, 1959; Marshall & McWilliam, 1982; Kitchener et al., 1990; Richards, 1995; Birt et al., 1997). With a diet that contains substantial amounts of fruit and occasionally leaves, most of these pteropodids are feeding generalists, much like New World phyllostomids such as Phyllostomus and Artibeus.

Based on this taxonomic overview, the New World tropics and subtropics contain more species of ecologically specialized nectar-feeding birds and bats than do Africa, Asia, or Australasia, but this diversity is concentrated in only two families (Trochilidae and Phyllostomidae), whereas in the geologically and biogeographically more complex Old World tropics and subtropics, this diversity occurs in more families and subfamilies. Because most honeyeaters, lorikeets and pteropodids are Australasian, this region contains the greatest taxonomic diversity of Old World vertebrate nectarivores. With its substantial radiation of sunbirds, Africa contains the next highest diversity, and Asia the least (Table 1).

The higher regional diversity of nectar-feeding vertebrates in the New World compared with the Old World also occurs at the local community or assemblage level (Table 2). Based on nine lowland New World sites and eight lowland Old World sites (four in Africa, two in Australia, and one each in Malaysia and Papua New Guinea), New World avian species richness is significantly greater than Old World species richness (12.8 vs. 7.9 species; Wilcoxon signed ranks test; $P = 0.011$) (Table 2a). The difference in species richness in New and Old World bat

Table 2 Summary of species richness of vertebrate pollinator assemblages in lowland tropical forests. In (a) we compiled data from as many community studies as we could find in the literature; bird and bat studies were independent of each other. In (b) we specifically chose well-studied sites for which lists of both nectar-feeding birds and mammals were available.

Location	Taxon	No. sites	Mean ± SE (range)
(a) Different sites for birds and bats by hemisphere			
New World	Birds	9	12.8 ± 1.9 (8–22)
New World	Bats	14	4.4 ± 0.3 (2–6)
Old World	Birds	8	7.9 ± 1.7 (3–18)
Old World	Bats	4	2.3 ± 0.5 (1–3)
(b) Same sites for birds and bats by hemisphere			
New World	Birds	6	17.0 ± 2.4 (11–24)
New World	Bats	6	5.2 ± 0.8 (3–8)
Old World	Birds	5	11.6 ± 2.4 (4–19)
Old World	Bats	5	1.6 ± 0.2 (1–2)

Sources of data: (a) Fleming (2005, Appendix), Simmons and Voss (1998, Table 75); (b) T. Fleming & J. Kress (in prep.).

assemblages is not significant (4.4 vs. 2.3 species; $P = 0.194$). Analysing only those sites for which we have both bird and bat data produces the same results (Table 2b). For both birds and bats, New World sites are richer than Old World sites, although only the bird means (technically, medians) differ significantly (17.0 vs. 11.6 species; $P = 0.008$); differences in the bat means approach significance (5.2 vs. 1.6 species; $P = 0.068$). Overall, New World lowland tropical sites contain up to 24 species of nectar-feeding birds and eight species of nectar-feeding bats; Old World sites contain up to 19 species of nectar-feeding birds and three species of (dedicated) nectar-feeding bats. Restricting the avian comparison to hummingbirds and their closest Old World counterparts, sunbirds, New World tropical and subtropical sites over a broad range of habitats contain three to 28 species of hummingbirds, whereas Old World sites contain three to seven species of sunbirds in Africa and up to six species in Borneo (Rebelo, 1987; Yumoto et al., 1997; Fleming et al., 2005). Again, the New World appears to be richer in species of morphologically specialized vertebrate pollinators than the Old World.

PATTERNS OF MORPHOLOGICAL DIVERSITY

In this section we describe hemispheric differences in vertebrate nectar-feeders with respect to size and morphological diversity. Our basic question here is: are New World nectar-feeders more diverse morphologically than their Old World counterparts? In terms of overall size, New World birds and bats are significantly smaller than their Old World counterparts (Table 3). On average, hummingbirds weigh less than half as much as sunbirds and less than one-fifth as much as honeyeaters. As a result of their small size and specialized flight morphology (Altshuler & Dudley, 2002; Altshuler et al., 2004; Stiles et al., 2005), most hummingbirds hover when they visit flowers, whereas passerines such as sunbirds and honeyeaters usually perch on flowers or branches while feeding, although hovering is known to occur in some species (Pyke, 1980; Stiles, 1981; Westerkamp, 1990; Dreisig, 1997; Cheke & Mann, 2001). A similar difference characterizes New and Old World nectar bats. Glossophagine nectar bats average only one-third the mass of pteropodid nectar bats (Table 3) and typically hover while visiting flowers (von Helversen, 1993; Stockwell, 2001; von Helversen & Winter, 2003). In contrast, pteropodids

nearly always land on flowers or branches near flowers to feed (e.g. Start & Marshall, 1976; Gould, 1978; Marshall & McWilliam, 1982; Westerkamp, 1990; Richards, 1995). These differences in mass and hovering ability have important implications for the evolution of flower or inflorescence sizes and their nectar rewards (Cruden et al., 1983; Opler, 1983; Pellmyr, 2002). Opler (1983), for example, showed that flower size and nectar volume are positively correlated with pollinator size in the flora of western Costa Rica. Plants whose flowers are visited by perching birds must also provide a perch near flowers or inflorescences sturdy enough to support them (Westerkamp, 1990).

In addition to differences in mass and hovering ability, New and Old World vertebrate nectarivores differ in the diversity of their trophic apparatus (i.e. bill or jaw size and shape). To support this generalization, we will focus mostly on hummingbirds and sunbirds as well as on phyllostomid and pteropodid bats. Overall, the morphological diversity of Old World nectar-feeding birds is substantial, reflecting their taxonomic (familial) diversity, but we restrict our attention here to each hemisphere's closest ecological counterparts. The New World has no close ecological analogues of lorikeets, but certain New World orioles and paruline warblers resemble Old World honeyeaters and white-eyes, respectively, in their feeding ecology (Stiles, 1981).

We present a simple ordination based on generic means of relative bill or jaw size and body size of hummingbirds vs. sunbirds and of phyllostomid vs. pteropodid bats in two-dimensional morphospace in Fig. 1. Our measure of relative bill size in birds is the ratio of bill length to wing chord length, a standard measure of body size in birds, based on data in Cheke & Mann (2001) and Fleming et al. (2005). Our measure of relative jaw size in bats is the ratio of jaw length to jaw width; forearm length is a standard measure of body size in bats. These data come from Andersen (1912) and Swanepoel & Genoways (1979). This plot indicates that the two-dimensional morphospaces occupied by hummingbirds and phyllostomid bats are greater than those occupied by sunbirds and pteropodids, respectively, which parallels differences in their taxonomic (generic and species) richness (Fig. 1).

We used coefficients of variation (CVs) of the mean of generic means to quantify differences in bill or jaw vs. body size morphospace in these animals (Table 4). A larger CV

Table 3 Summary of body-mass data and hovering ability for nectar-feeding birds and bats.

Family	Hemisphere	No. species	Mass (g) ± 1 SE (range)	Hovering flight?
Phyllostomidae (glossophagines)	NW	35	13.3 ± 0.91 (7.5–30.0)	Yes
Pteropodidae ('macroglossines')	OW	12	37.7 ± 6.7 (13.2–82.2)	No
Trochilidae	NW	251	5.2 ± 0.14 (2–20.2)	Yes
Psittacidae (lories)	OW	19	91.9 ± 15.0 (20.2–240)	No
Meliphagidae	OW	111	33.4 ± 3.0 (7.4–152.0)	Rarely
Zosteropidae	OW	23	12.1 ± 1.1 (7.9–30.0)	No
Nectariniidae (sunbirds)	OW	61	11.3 ± 0.8 (4.7–38.4)	Rarely

Sources of mass data: bats – Bonaccorso (1998), Fleming et al. (2005), Nowak (1994); birds Dunning (1993). Abbreviations: NW, New World; OW, Old World.
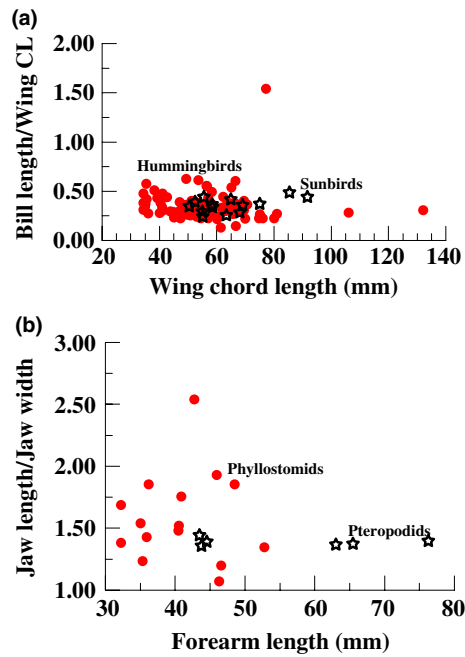
Figure 1 Ordination of genera of (a) hummingbirds and sunbirds, and (b) glossophagine and 'macroglossine' bats in two-dimensional morphological space. Mean values for New World genera are indicated by solid circles, and for Old World genera by open stars.

means that a group occupies a larger morphospace. In the hummingbird–sunbird comparison, the CV of each of the three morphological variables was significantly greater in hummingbirds, even after controlling for differences in the number of genera in the two families; relative bill length was 2.2 times more variable in hummingbirds. Similarly, except for forearm length (Fig. 1), phyllostomid bats were significantly more variable than pteropodids after controlling for differences in number of genera; relative jaw length was 11 times more variable in phyllostomids. It is worth noting that hummingbirds are also substantially more variable in bill length (in both absolute and relative terms) than Old World honeyeaters and lories, based on data in Rand & Gilliard (1967) (Table 4). In summary, these results support the

hypothesis that New World nectar-feeding birds and bats occupy a larger ecological morphospace, at least in terms of their bills and jaws, than their closest Old World ecological counterparts.

While they will not be a main focus of this paper, we note that Hawaiian honeycreepers (Fringillidae: Drepanidini) are also well known for their morphological diversity. Classified in 22 genera containing about 47 species, this clade includes at least three genera with long, decurved bills for nectar-feeding: *Akialoa* with five species; *Vestaria* with one species; and *Drepanis* with two species (Ziegler, 2002). An additional two genera (*Loxops* with seven species; *Himatione* with one species) are also highly nectarivorous. Overall, this island clade contains substantially more morphological diversity than an equivalent number of genera or species of sunbirds and honeyeaters.

PATTERNS OF PLANT DIVERSITY

If New World nectar-eating birds and bats are more diverse in terms of species richness and range of morphologies than their Old World counterparts, is this also true of their food plants? Have a greater number or proportion of plant clades (families) or growth forms evolved bird or bat flowers in the New World than elsewhere? Are there hemispheric differences in the degree of phenotypic specialization in vertebrate-pollinated flowers? And have plant genera partitioned nectar-feeding birds and bats more finely in the New World than in the Old World? If this is true, we might expect to find more examples of New World plant genera that contain species that are bird-pollinated and species that are bat-pollinated than in the Old World. To address these questions, we will initially restrict our analysis to two groups of close ecological counterparts: hummingbirds and sunbirds, and phyllostomid and pteropodid bats. Following this, we will broaden our comparison to include other families of Old World nectar-feeding birds.

Hummingbirds vs. sunbirds

Overall, hummingbirds are known to visit the flowers of at least 311 genera in 95 families, based on dietary data summarized by Schuchmann (1999). These 95 families repre-

Table 4 Morphological variation in six groups of tropical nectar-feeding vertebrates as reflected by coefficients of variation (CV) in absolute and relative bill or jaw size and body size; CVs were calculated based on generic means.

Morphological variable	Hummingbirds (n = 90 genera)	Sunbirds (n = 14 genera)	Honeyeaters (n = 19 genera)	Lories (n = 9 genera)	Phyllostomid bats (glossophagines) (n = 15 genera)	Pteropodid bats ('macroglossines') (n = 6 genera)
Wing chord length or forearm length	0.268 (0.235–0.295)†	0.192	0.314	0.247	0.154 (0.140–0.168)‡	0.251
Jaw or bill length	0.607 (0.413–0.702)	0.361	0.344	0.247	0.195 (0.187–0.227)	0.165
Relative bill or jaw length*	0.446 (0.329–0.537)	0.203	0.225	0.047	0.231 (0.208–0.272)	0.021

*Calculated as bill length/wing chord length; relative jaw length was calculated as jaw length/jaw width.
†95% confidence limits based on 25 bootstraps of 14 genera/sample.
‡95% confidence limits based on 25 bootstraps of 6 genera/sample.

sent about 56% of the 169 subtropical and tropical New World plant families listed in Heywood (1993); excluded from the Neotropical family list are aquatic and grass-like families. In terms of the number of genera producing hummingbird-visited flowers, the top five plant families and their growth habits are Fabaceae (especially mimosoid legumes) (34 genera; mostly trees), Acanthaceae (17; herbs), Bromeliaceae (14; epiphytes), Rubiaceae (14; mostly shrubs), and Lamiaceae (13; herbs) (Schuchmann, 1999). In terms of the number of hummingbird genera visiting flowers of a particular family, the top five plant families are Fabaceae (especially the mimosoids) (108 bird genera), Rubiaceae (78), Ericaceae (65; herbs and shrubs), Bromeliaceae (49), and Malvaceae (44; shrubs). Depending on habitat, tropical hummingbirds locally visit from 18 to 85 species of flowers in eight to 25 families (Stiles, 1981; Arizmendi & Ornelas, 1990; Buzato et al., 2000). Relatively high species-specificity, at least in terms of bill and corolla length, is characteristic of hummingbird plants in most tropical habitats. Thus, short-billed trochilines tend to visit short-corolla flowers, and hermits with long, curved bills tend to visit flowers with long, curved corollas (e.g. *Heliconia*)

(Stiles, 1981; Feinsinger et al., 1985; Fleming et al., 2005). In terms of plant habits, the most common hummingbird plant types are herbs and epiphytes, which account for nearly 60% of the flower species visited by these birds in nine habitats (Table 5). Only about 10% of the species visited by hummingbirds in these habitats are trees. Finally, flower types visited by these birds are overwhelmingly tubular in shape (Table 6).

Like hummingbirds, sunbirds visit a wide variety of flowers in at least 279 genera in 94 families (Cheke & Mann, 2001). These 94 families represent about 59% of the 159 subtropical and tropical African plant families listed in Heywood (1993). They visit flowers in 10 or more genera in five plant families of several different growth forms: Fabaceae (especially mimosoid legumes) (34 genera; trees), Rubiaceae (19; shrubs), Lamiaceae (15; herbs), Loranthaceae (15; hemiparasites), and Bignoniaceae (11; trees or vines). Based on the number of sunbird genera visiting their flowers, the top five families are Fabaceae (11 bird genera), Loranthaceae (11), Lamiaceae (10), Bignoniaceae (9), and Aloaceae (6; herbaceous succulents). Depending on habitat, they locally visit flowers of five to 45 species of

Table 5 Food plants of tropical and subtropical nectar-feeding birds and bats by growth habit.

Pollinator taxon	Number of habitats	Number of plant taxa by habit (proportion)					
		Herbs	Vines or climbers	Epiphytes	Shrubs	Trees	Total
Hummingbirds	9*	79 (0.27)	38 (0.13)	96 (0.32)	54 (0.18)	29 (0.10)	296 species
Sunbirds	Many†	30 (0.31)	14 (0.14)	3 (0.03)	25 (0.26)	26 (0.26)	98 families§
Glossophagine bats	7*	1 (0.02)	11 (0.17)	18 (0.28)	4 (0.06)	30 (0.47)	64 species
'Macroglossine' bats	Many‡	4 (0.05)	1 (0.01)	2 (0.02)	4 (0.05)	76 (0.87)	87 genera

Sources of data: Hummingbirds and phyllostomid bats – Fleming et al. (2005); sunbirds – Cheke & Mann (2001); pteropodid bats – Mickleburgh et al. (1992).

*Unit of replication is plant species.

†Unit of replication is plant family.

‡Unit of replication is plant genus.

§This number includes four families with more than one growth form.

Table 6 Flower types visited by tropical vertebrate pollinators.

Taxon	Habitat and country	Plant taxon tallied	Number of flower types by plant taxon (proportion)					
			Open or cup	Tubular	Gullet or bell	Flag	Shaving brush	Total taxa
Hummingbirds	Paramo, Costa Rica	Species	5 (0.26)	14 (0.74)	0	0	0	19
	Atlantic rain forest, Brazil	Genus	3 (0.07)	31 (0.72)	2 (0.05)	7 (0.16)	0	43
	Dry forest, Mexico	Genus	3 (0.25)	9 (0.75)	0	0	0	12
	Rain forest, Trinidad	Genus	7 (0.15)	27 (0.61)	2 (0.05)	2 (0.05)	6 (0.14)	44
Sunbirds	Fynbos, South Africa	Genus	3 (0.04)	43 (0.62)	8 (0.11)	5 (0.07)	11 (0.16)	70
	Montane forest and shrublands, Central Africa	Genus	0	17 (1.00)	0	0	0	17
	Rain forest, Borneo	Species	0	9 (1.00)	0	0	0	9
Glossophagine bats	Various	Genus	1 (0.02)	15 (0.28)	28 (0.52)	2 (0.04)	8 (0.15)	54
'Macroglossine' bats	Various	Genus	3 (0.07)	9 (0.20)	7 (0.16)	2 (0.05)	23 (0.52)	44

Sources of data: Hummingbirds – Snow & Snow (1972), Wolf et al. (1976), Arizmendi & Ornelas (1990), Buzato et al. (2000). Sunbirds – Rebelo (1987), Dowsett-Lemaire (1989), Yumoto et al. (1997), Yumoto (2005). Bats – Dobat & Peikert-Holle (1985).

plants in up to 17 families (Pettet, 1977; Rebelo, 1987; Noske, 1995; Yumoto *et al*., 1997; Sakai 2000). The overall distribution of growth forms in plant families visited by sunbirds is similar to that of hummingbirds, despite differences in our units of replication (species for hummingbirds and families for sunbirds) (Table 5). Both groups visit many genera and species of herbs, vines, and shrubs. Epiphytes (e.g. Bromeliaceae) are especially common in the Neotropics (Gentry, 1982; Benzing, 2000), and they provide an important food source for hummingbirds. Except for one genus (*Pitcairnia*) in West Africa, bromeliads are absent from the Old World, which probably accounts for the low proportion of epiphytes visited by sunbirds. Based on species accounts in Cheke & Mann (2001), it appears that forest-dwelling sunbirds are more likely to feed at flowers produced by canopy or subcanopy trees than are hummingbirds. They often visit these flowers in mixed-species flocks, a behaviour that is unknown in hummingbirds. In terms of flower types, sunbirds resemble hummingbirds in that they visit many kinds of tubular flowers produced by herbs, vines, epiphytes, and shrubs (Table 6).

Hummingbirds and sunbirds share about two-thirds (61) of the 94–95 plant families on their food lists. Of the 33–34 unique plant families for each bird family, only five hummingbird families (15%) are New World endemics and only eight sunbird families (24%) are Old World endemics. Thus, most unique families for both hummingbirds and sunbirds are pantropical in distribution but produce bird-pollinated flowers in only one hemisphere. Pantropical families that produce flowers visited only by hummingbirds include Begoniaceae, Caprifoliaceae, Gesneriaceae, Heliconiaceae, and Polemoniaceae. Pantropical families that produce flowers visited only by sunbirds include Araliaceae, Arecaceae, Chrysobalanaceae, Ebenaceae, and Theaceae.

Phyllostomid vs. pteropodid bats

Based on data in Dobat & Peikert-Holle (1985), nectar-feeding bats appear to visit flowers in far fewer families than do hummingbirds and sunbirds. Of a total of 58 families whose flowers are visited by nectar bats, at least 43 are visited by phyllostomids and 28 are visited by pteropodids; 13 of the 58 families (22%) have flowers that are visited by both families of bats. Twice as many plant families (30 vs. 15) are unique to phyllostomids. Six of the unique phyllostomid families (20%) are New World endemics, and four of the pteropodid families (27%) are Old World endemics. As for hummingbirds and sunbirds, most of the unique families are pantropical in distribution but only produce bat-pollinated flowers in one hemisphere. For phyllostomids, these families include Acanthaceae, Capparaceae, Gesneriaceae, Malvaceae, and Solanaceae; for pteropodids, they include Apocynaceae, Loranthaceae, and Rosaceae.

In terms of the number of genera producing phyllostomid bat-visited flowers, the top five families and their growth habits are Cactaceae (25 genera; large succulents), Bignoniaceae (15; trees or vines), Bombacaceae (14; trees), Myrtaceae (11; trees),

and Fabaceae (i.e. caesalpinaceous legumes) (10; trees); for pteropodids, the top five families are Myrtaceae (10 genera), Bignoniaceae (6), Arecaceae (5, palms), Bombacaeae (5), and Fabaceae (*sensu stricto*) (5; trees). Although both families of bats visit many flowers produced by trees, pteropodid feeding appears to be much more strongly associated with tree flowers than is the case for phyllostomids (Table 5). Like hummingbirds, phyllostomids feed at many species of epiphytes and vines. Finally, in terms of flower types, phyllostomid-visited flowers tend to be more phenotypically specialized. Flowers in about 80% of the genera visited by phyllostomids are tubular or bell-shaped, compared with only about 36% of the genera visited by pteropodids; nearly 60% of pteropodid flowers occur in genera with cup-shaped or shaving-brush flowers (Table 6). The proportion of genera containing flowers with restricted morphologies (i.e. tubular or bell-shaped) is significantly higher in phyllostomids (χ^2 = 17.2, d.f. = 1, $P < 0.0001$). Thus, flowers visited by phyllostomids appear to have undergone greater evolutionary specialization, on average, than those visited by pteropodids.

Lories and honeyeaters

The major avian pollinators in the Australasian region are brush-tongued parrots (Psittacidae: Loriinae) and honeyeaters (Melaphagidae). Fossil evidence (parrots only; Forshaw, 2006) and molecular evidence (Barker *et al*., 2004) indicate that these two families first evolved in the early Cenozoic and are thus much older than sunbirds, the most specialized Old World avian nectar-feeders (Stiles, 1981). Despite their substantial evolutionary ages, neither of these groups of birds is as specialized in its ecological relationships with plants as are hummingbirds and sunbirds. Lorikeets, especially, appear to be generalized flower visitors that feed at open, cup-like, or shaving-brush flowers produced by trees and shrubs. Eucalypts (*Eucalyptus*, *Corymbia*) are particularly important nectar sources for these gregarious and highly mobile birds (Franklin & Noske, 2000; Forshaw, 2006).

All or most species of honeyeaters visit flowers, but the degree of ecological specialization on nectar as a food source varies considerably among species. Among the 70 species of Australian honeyeaters (Ford *et al*., 1979), smaller species and genera tend to be more nectarivorous than larger species and genera, which tend to be more frugivorous or omnivorous (Pyke, 1980). According to Pyke (1980), species in four genera (*Myzomela, Certhionyx, Acanthorhynchus*, and *Lichmera*) are highly nectarivorous, and two additional genera (*Phylidonyris, Melithreptus*) are nearly as nectarivorous. In the heathlands, woodlands, and forests of eastern Australia, honeyeaters visit over 250 species of plants in over 40 genera and 25 families (about one-quarter of the number of families visited by hummingbirds and sunbirds) (Ford *et al*., 1979; Paton, 1986). These families represent only about 17% of the 144 non-aquatic and non-grass-like Australian plant families listed in Heywood (1993). Honeyeaters thus visit flowers in proportionately fewer plant families in their flora than do either hummingbirds or

sunbirds (χ^2 tests, $Ps < 0.0001$). Major plant families providing nectar resources for honeyeaters include Myrtaceae (10 genera; trees and shrubs), Proteaceae (7; trees and shrubs), Loranthaceae (6; hemiparasites), Rutaceae (6; trees and shrubs), and Epacridaceae (5; shrubs); other important families in south-eastern Australia include Myoporaceae, Xanthorrhoeaceae, Haemodoraceae, and Fabaceae (Ford *et al.*, 1979).

A quantitative summary of the kinds of plants and flowers visited by tropical honeyeaters is provided in Table 7. In lowland rain forest in Papua New Guinea, 17 species of honeyeaters were recorded visiting flowers of 17 species of plants in 12 genera and 9 families (Brown & Hopkins, 1995). Most flowers were produced by canopy trees, and cup-shaped and tubular flowers were the most common flower types. In woodland habitats of north-western Australia, 21 species of honeyeaters visited flowers of 112 species in 53 genera and 27 families (Franklin & Noske, 2000). Trees are the most common

growth form in these species, and the most common flower types are easily accessible and non-restrictive (i.e. small in size, cup-shaped, or brush-like). Thus, unlike many hummingbirds and sunbirds, honeyeaters tend to visit easily accessible flowers produced by large woody plants in both New Guinea and northern Australia (Brown & Hopkins, 1995; Franklin & Noske, 2000). In Australia, flowers of the Myrtaceae and Proteaceae have been particularly important in honeyeater evolution (Ford *et al.*, 1979).

In Table 8 we summarize our results with respect to expected hemispheric differences in plants based on our initial hypothesis (i.e. that plant–pollinator interactions have undergone greater evolutionary specialization more frequently in the New World than in the Old World). Tests of three predicted differences require comparisons of New and Old World ecological counterparts (i.e. hummingbirds vs. sunbirds, and phyllostomid vs. pteropodid bats). When we do this, no striking differences between hummingbirds and sunbirds and

Table 7 Summary of honeyeater–plant relationships in two Australasian localities. The most common growth forms and flower types are indicated in bold.

Habitats	Number of honeyeater species	Number of plant taxa	Number of genera by growth form (proportion)	Number of genera by flower type (proportion)
Lowland rain forest, Papua New Guinea	17	Families – 9 Genera – 12 Species – 17	Epiphytic vine – 1 (0.08) Small tree – 1 (0.08) **Canopy tree – 11 (0.84)**	**Tube – 5 (0.36)** **Cup – 5 (0.36)** Knob –1 (0.07) Tiny clusters –3 (0.21)
Open woodland, monsoon forest, and mangroves, north-western Australia	21	Families – 27 Genera – 53 Species – 112	Herb – 1 (0.02) Climber – 4 (0.07) Woody parasite –5 (0.09) Shrub –15 (0.27) **Small tree –18 (0.32)** Large tree –13 (0.23)	Tube –8 (0.15) Gullet –1 (0.02) Flag –6 (0.11) Brush or open cup –15 (0.27) Others: **small –18 (0.33)**; large – 7 (0.13)

The number of genera by growth form and flower type exceeds the number of genera when species within genera exhibit different growth habits or flower types.
Sources of data: Brown & Hopkins (1995), Franklin & Noske (2000).

Table 8 Summary of predicted differences in the evolutionary specialization of plants pollinated by birds and bats in the New and Old World tropics and subtropics. These predictions follow from the hypothesis that plants in the New World have evolved more specialized relationships with their vertebrate pollinators than plants in the Old World.

Predicted difference	Results
1. NW nectar-feeders pollinate flowers of more families and genera than do their OW counterparts	Birds: HBs (95 families) = SBs (94) ≠ HEs (25-27) Bats: Phyllos (43) ≠ Pteros (28)
2. NW nectar-feeders pollinate flowers of a greater range of plant habits than do their OW counterparts (proportion non-trees)*	Birds: HBs (0.90) ≥ SB (0.74) >> HEs (0.38) Bats: Phyllos (0.53) > Pteros (0.13)
3. NW nectar-feeders visit more flowers with restrictive morphologies than do their OW counterparts (proportion tubular or gullet flowers)†	Birds: HBs (0.73) ≤ SBs (0.91) >> HEs (0.19) Bats: Phyllos (0.36) ≥ Pteros (0.12)

Abbreviations: NW, New World; OW, Old World. HB, hummingbirds; HE, honeyeaters; Phyllo, phyllostomid bats; Ptero, pteropodid bats; SB, sunbirds. Based on χ^2 tests, = or ≥ means $P > 0.05$; > or >> means $P < 0.05$; no tests conducted for prediction 1.
*Based on data in Tables 5 and 7.
†Based on data in Tables 6 and 7.

their food plants emerge. Both families of birds visit flowers in similar numbers of families and genera and similar proportions of families in their floras; they visit primarily tubular flowers that tend to exclude other kinds of pollinators; and they visit many flowers produced by herbs and vines as well as flowers produced by trees. From this, we reject our initial hypothesis and accept the null hypothesis of no difference in the extent to which New and Old World plants have specialized on hummingbirds and sunbirds, respectively. Although hummingbirds exhibit greater species richness and higher morphological diversity than sunbirds (probably as a result of their greater evolutionary age), their food plants have apparently not evolved a greater degree of evolutionary specialization to them than have the food plants of sunbirds.

A different conclusion emerges when we compare the food plants of phyllostomid and pteropodid bats. The two families do appear to differ in the number of plant families they visit as well as in the kinds of plants and flowers they visit. Phyllostomid bats visit flowers from more families, a greater range of plant habits, and a higher proportion of families producing flowers with restrictive morphologies than do pteropodid bats. Given these differences, we accept our initial hypothesis that New World plants appear to have undergone greater evolutionary specialization for bat pollination than Old World plants. Interestingly, honeyeaters appear to resemble pteropodid bats more than sunbirds in the degree of evolutionary specialization of their food plants. Like pteropodids, honeyeaters visit flowers produced by a lower number (and proportion) of plant families; they concentrate their feeding at flowers produced by trees; and they tend to forage at easily accessible flowers that are sometimes also visited by pteropodid bats (e.g. Woodside & Pyke, 1985; Crome & Irvine, 1986; Law & Lean, 1999).

Our final predicted hemispheric difference is that New World plants exhibit a greater number of families and genera containing 'split pollinator personalities'. Based on data in

Table 9, this hypothesis is supported. Three times as many genera (in twice as many families) of New World plants contain both bird- and bat-pollinated species than is the case for Old World plants. With seven 'split' genera, the New World family Bromeliaceae contains an especially high number of bird- and bat-pollinated genera. Five New World families contain two or more such genera, compared with only one Old World family.

DISCUSSION

Our major objective in this paper was to compare the adaptive radiations of nectar-feeding birds and bats in the New and Old World tropics with respect to patterns of species richness, morphological diversity, and degree of feeding specialization as mediated by the degree of evolutionary specialization in their food plants. While our overall results support our initial hypothesis that New World birds and bats and their food plants tend to be more specialized than their Old World counterparts, our analysis has also revealed that there are significant biogeographical differences in the degree of evolutionary specialization among Old World avian nectar-feeders. Thus, sunbirds, whose major radiation has taken place in Africa (Irwin, 1999), are phenotypically and ecologically more specialized than Australasian honeyeaters. Similarly, pteropodid bats, which originated in Asia–Australasia, resemble honeyeaters in being less specialized phenotypically and ecologically than their New World counterparts.

Our major results are summarized in Fig. 2, in which we propose that plant–vertebrate pollinator evolution has proceeded along somewhat different trajectories in three major tropical regions. From west to east, these regions include: the Neotropics; sub-Saharan Africa and seasonal Asia; and aseasonal Southeast Asia and Australasia. The degree of feeding niche specialization in these regions, as reflected by diet and feeding morphology, decreases in a west → east fashion. Thus, vertebrate nectar-feeders in the Neotropics can be character-

Table 9 Families and genera of plants that contain species that are specialized for either bird- or bat-pollination.

New World		Old World	
Family	Genus	Family	Genus
Acanthaceae	*Aphelandra*	Bombacaceae	*Adansonia, Durio*
Bromeliaceae	*Aechmea, Bromelia, Guzmania, Pitcairnia, Puya, Tillandsia, Vriesea*	Fabaceae	*Mucuna*
Cactaceae	*Pachycereus, Stenocereus*	Heliconiaceae	*Heliconia*
Caesalpinaceae (Fabaceae)	*Bauhinia*	Musaceae	*Musa*
Campanulaceae	*Burmeistera, Centropogon*	Pandanaceae	*Freycinetia*
Gesneriaceae	*Drymonia, Gesneria, Paliavana*	Proteaceae	*Banksia*
Lobeliaceae	*Siphocampylus*		
Malvaceae	*Abutilon*		
Marcgraviaceae	*Marcgravia*		
Mimosaceae	*Calliandra, Inga, Parkia*		
Passifloraceae	*Passiflora*		

Sources of data: Kress (1985), Itino *et al.* (1991), Endress (1994), Sazima *et al.* (1999), Buzato *et al.* (2000), J. Kress (personal communication).
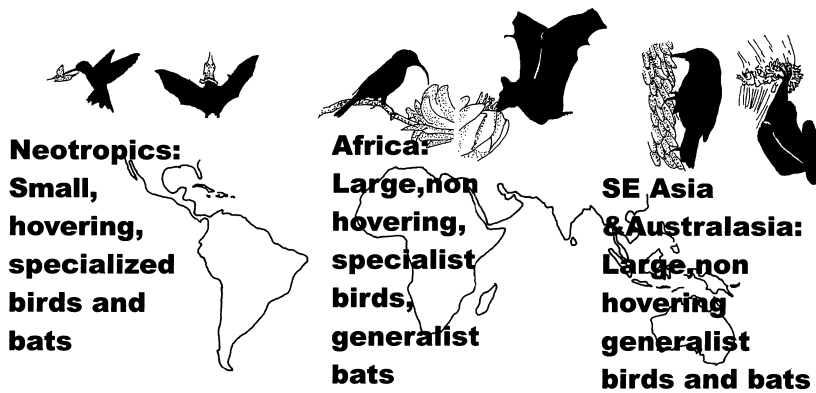
Figure 2 Summary of the major features of the adaptive radiations of nectar-feeding vertebrates. Foraging birds and bats include: Neotropics – a hummingbird and a glossophagine bat; Africa – a sunbird and a 'macroglossine' bat; Southeast Asia and Australasia – a honeyeater and a 'macroglossine' bat. Animals are not drawn to the same scale.

ized by their small size, ability to hover, and relatively specific relationships with their food plants. Two extreme examples of this specificity in hummingbirds are described by Snow & Snow (1980) and Temeles & Kress (2003). An extreme example for a phyllostomid bat is described by Muchhala (2006a). Sub-Saharan Africa contains one species of non-hovering nectar-feeding pteropodid bat and a relatively high diversity of larger, non-hovering sunbirds, which Stiles (1981) considered to be the second-most specialized group of nectar-feeding birds, and some of which exhibit specific relationships with certain flowers (e.g. South African asclepiads and orchids; Pauw, 1998; Johnson & Brown, 2004). Nectar-feeding vertebrates in Southeast Asia include a few sunbirds and pteropodid bats. In Australasia they include relatively large, non-hovering lorikeets and honeyeaters as well as pteropodid bats. All three of these groups tend to have non-specific feeding relationships with their food plants, except perhaps in the heathlands and sclerophyll woodlands of south-eastern Australia, where honeyeaters have evolved specific relationships with certain groups of plants (e.g. *Anigozanthos*, *Banksia*, Epacridaceae; Ford *et al.*, 1979). At a very gross level, therefore, the degree of evolutionary specialization between nectar-feeding birds and bats and their food plants decreases from the Neotropics through Africa and South Asia, to Southeast Asia and

Australasia. There is not a simple New World–Old World dichotomy in this evolution. Instead, there is substantial regional variation within the Old World tropics and subtropics in the degree of evolutionary specialization in both plants and their vertebrate pollinators.

What processes or factors are responsible for these broad biogeographical patterns? Why does the Neotropics harbour more phenotypically specialized vertebrate pollinators and more evolutionarily specialized plants, on average, than other regions? Why are plant–vertebrate pollinator interactions less specialized evolutionarily in Southeast Asia and Australasia? Although it undoubtedly takes time for specialized plant–pollinator relationships to evolve, we discount differences in the evolutionary ages of plants and their vertebrate pollinators as a major explanation for these differences for at least three reasons. First, it is not true that hummingbirds and glossophagine bats are older than their Old World counterparts (Fig. 3). While hummingbirds are likely to be evolutionarily older than sunbirds, their modern forms are not older than lorikeets and honeyeaters, yet they are clearly more diverse taxonomically and more specialized morphologically and behaviourally for flower visiting than the latter two families. Pteropodid bats are substantially older than phyllostomid bats (Teeling *et al.*, 2005; Jones *et al.*, 2005), and, except for
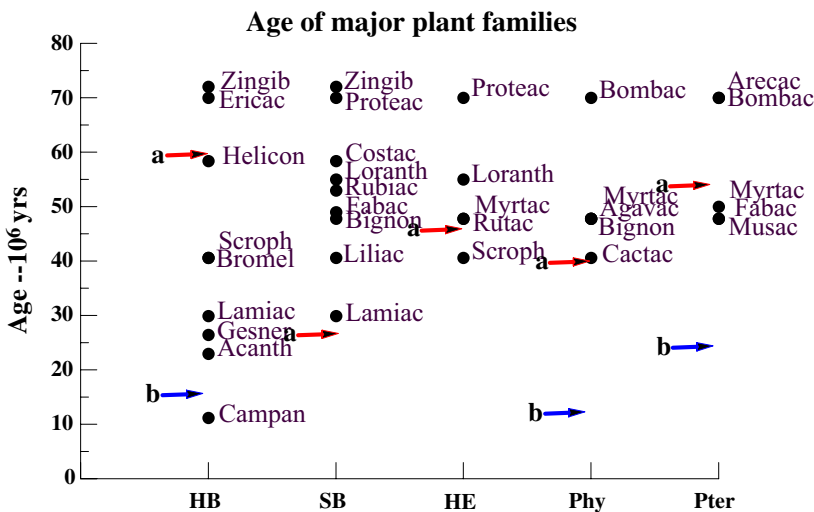

Figure 3 Evolutionary ages of major groups of nectar-feeding vertebrates and their food plants. Plant data are based on the fossil record; animal data are based on molecular-based phylogenies. Arrows labelled with an 'a' indicate the estimated time of origin of each vertebrate family; arrows labelled with a 'b' indicate the estimated time of radiation of extant (crown) forms. Sources of data: Barker *et al.* (2004), Bleiweiss (1998b), Collinson *et al.* (1993), Jones *et al.* (2005). Abbreviations: HB, hummingbirds; SB, sunbirds, HE, honeyeaters; Phy, phyllostomid bats; Pter, pteropodid bats.

Megaloglossus, nectar-feeding genera are not the most-derived (youngest) members of this family (Giannini & Simmons, 2005). Despite their greater evolutionary age, 'macroglossine' pteropodids have clearly undergone a much more modest radiation than the glossophagine phyllostomids. Second, it is not true that the major plant families containing flowers that are pollinated by vertebrates in the New World are older, on average, than Old World plant families with vertebrate-pollinated flowers. Except for a few families visited primarily by hummingbirds (e.g. Campanulaceae and Acanthaceae), most of the major plant families with flowers visited by nectar-feeding birds and bats are relatively similar in age and apparently evolved in the early Cenozoic, well before the appearance of modern groups of these pollinators (Fig. 3). Insects were probably the major pollinators in the basal lineages of many of these families (e.g. Ford *et al.*, 1979; Crepet & Friis, 1987; Endress, 1994). We will further discuss the implications of this below. Finally, the history of Hawaiian honeycreepers (Fringillidae, Drepanidini) indicates that it only takes a few million years to produce specialized nectar-feeding morphology. In less than 5 Myr, this group radiated into 22 genera and nearly 50 species, including several genera that are highly specialized morphologically for feeding at long-corolla, tubular flowers of Campanulaceae (Freed *et al.*, 1987; Tarr & Fleischer, 1995; Lovette *et al.*, 2001; Ziegler, 2002).

A second possible explanation for these patterns involves resource predictability in space and time. Specialized plant–pollinator mutualistic interactions are likely to evolve whenever floral resources are spatially and temporally predictable (Waser *et al.*, 1996; Ollerton *et al.*, 2006). If this is true, the following relationship should also be true: Neotropical floral resource spatio-temporal predictability (STP) ≥ African and South Asia STP > Southeast Asia and Australasian STP. That is, based on the degree of specialization of their vertebrate pollinators, we would expect to find evidence for highly predictable flowering seasons in the Neotropics, sub-Saharan Africa, and South Asia, and evidence for significantly more variable flowering seasons in Southeast Asia and Australasia. While a meta-analysis of flowering phenology studies is beyond the scope of this paper, published reviews of such data (e.g. Corlett & LaFrankie, 1998; Sakai, 2001; van Schaik & Pfannes, 2005) support this prediction. Sakai (2001) pointed out that annual flowering patterns are widespread in Neotropical forests (e.g. see Stiles, 1977, for a classical example of the regularity of hummingbird-pollinated *Heliconia* flowering seasons in a Costa Rican rain forest), whereas supra-annual flowering seasons are widespread in the aseasonal lowlands of Southeast Asia. Non-annual flowering patterns are also common in trees in lowland and montane Papua New Guinea (Brown & Hopkins, 1995; Wright, 1998). In contrast to the supra-annual flowering behaviour of canopy trees in lowland Borneo, gingers and mistletoes exhibit more continuous year-round flowering and have evolved relatively specialized pollinator relationships with a few species of sunbirds (Yumoto *et al.*, 1997; Sakai, 2000). Flowering in Australian eucalypts, which are major foods for honeyeaters, lorikeets, and ptero-

podid bats, is also notoriously variable in space and time, and this phenology has selected for generalized diets and high mobility in their pollinators (Paton & Ford 1977; Paton, 1986; Franklin & Noske, 2000; Palmer *et al.*, 2000; Woinarski *et al.*, 2000; Vardon *et al.*, 2001). Like the case for the Neotropics, the flowering phenology of African tropical plants does not feature general flowering (masting) events but instead involves annual flowering cycles (van Schaik & Pfannes, 2005). A similar pattern holds for seasonal parts of Asia (Corlett & LaFrankie, 1998).

A third possible explanation for these patterns involves the cost of producing vertebrate-pollinated flowers. Given their large size and high energetic demands relative to most insect pollinators, birds and bats are expensive pollinators. Assuming that most bird and bat pollination systems have evolved from insect-pollinated flowers (e.g. Crepet & Friis, 1987; Endress, 1994; Grant, 1994; Proctor *et al.*, 1996), it follows that plants will evolve vertebrate-pollinated flowers more often if flower costs in terms of size, structure, and nectar reward do not differ substantially from the costs of insect-pollinated flowers. This will be especially true if the benefits of vertebrate pollination in terms of pollen deposition and removal are substantially greater than flower costs. A flower adapted to pollinators with hovering flight can be small and delicate relative to a flower that needs to support the full weight of a pollinator. Thus, flowers in the New World that are pollinated by hovering glossophagines and hummingbirds might be expected to evolve from small insect-pollinated flowers more readily than flowers that need to support relatively heavy, non-hovering vertebrate pollinators in the Old World (von Helversen, 1993). Hummingbird pollination, for example, has evolved numerous times from insect pollination in the mountains of western North America, presumably because of the low cost of this transition relative to its benefit (Grant, 1994; Wilson *et al.*, 2006). Similarly, several genera of bromeliads (e.g. *Tillandsia*, *Vriesia*, *Pitcairnia*) have independently evolved insect-, bird-, or bat-pollinated flowers numerous times (Benzing, 2000). This flexibility suggests that the evolutionary costs behind these pollinator switches are not particularly high relative to their benefits. In contrast, the non-hovering flight and large body sizes of many kinds of Old World nectar-feeding birds and bats (and also non-glossophagine phyllostomids) should make them less attractive 'targets' for the evolution of specialized bird- or bat-flowers. We might expect plants to evolve easily accessible flowers (e.g. shaving brushes), rather than flowers with restrictive morphology (e.g. tubular or gullet-shaped), to attract relatively large vertebrate nectar-feeders as well as other pollinators. In support of this, von Helversen (1993) indicated that non-glossophagine phyllostomids such as *Phyllostomus discolor* and *Artibeus jamaicensis*, which weigh up to 50 g and which do not hover at flowers, typically pollinate flowers produced by trees that are either large (*Ochroma*) or brush-like (*Parkia*, *Hymenaea*). In contrast, except for cactus flowers, glossophagine bats often pollinate small, delicate flowers produced by epiphytes (e.g. many bromeliads, *Burmeistera*) or flowers that are presented in

pendulous fashion (e.g. *Markea*) (von Helversen, 1993; Muchhala & Jarrín, 2002; Muchhala, 2006b).

A further possible explanation for this pattern is that New World birds and bats have more evolutionary potential (i.e. are less constrained genetically) to develop a diverse array of morphologies and mutualistic relationships with their food plants than Old World birds and bats. This hypothesis has been used to explain why cardueline finches (Fringillidae: Carduelini) in Hawaii underwent a much more extensive adaptive radiation, producing the Hawaiian honeycreepers (Drepaniini), than did thrushes (Muscicapidae: Turdinae). World-wide, cardueline finches are morphologically more variable than thrushes, and this evolutionary flexibility apparently allowed them to evolve into an impressive set of new feeding niches when they reached the Hawaiian Islands (Lovette *et al.*, 2001; Ziegler, 2002). Similarly, Stiles (2004) used this argument to explain why hermit hummingbirds are restricted to lowland tropical habitats whereas trochilines have radiated extensively at mid-to-high elevations. Unlike hermits, trochiline morphology, including overall size, bill size, and wing size and shape, varies significantly with elevation in response to changes in the physical and biological environment. What has constrained hermits from doing this is currently unknown.

Rigorously testing this hypothesis for other nectar-feeders is beyond the scope of this paper. We note, however, that pteropodid bats are not inherently less variable morphologically than plant-visiting phyllostomids. Pteropodids that are mostly frugivorous, for example, occupy a much larger morphospace than frugivorous phyllostomids (Muscarella & Fleming, 2007). Only nectar-feeding pteropodids exhibit constrained morphology and have undergone a modest evolutionary radiation. We suspect that this constraint is more ecological than evolutionary in pteropodids as well in other Old World nectar-feeders, including sunbirds, honeyeaters, and lorikeets. That is, the 'ecological theatre', which includes flower types and patterns of resource availability in space and time, has been a stronger constraint on morphological variability and behaviour in these animals than has their genetic constitution. The presence of Bromeliaceae in the New World, for example, has provided an important resource base for small, hovering vertebrate pollinators that is largely absent in the Old World.

CONCLUSIONS

Our initial hypothesis in this study was that vertebrate pollination systems have undergone greater evolutionary specialization more frequently in the New World tropics than in the Old World tropics, and we predicted that New World pollination systems would contain more species, greater morphological diversity, and a higher degree of evolutionary specialization in their food plants. The results of our analyses generally support this hypothesis and its predictions. Not included in our initial hypothesis was the existence of a substantial difference within the Old World

tropics, in that Africa displays a greater degree of evolutionary specialization, at least in its nectar-feeding birds, than do Southeast Asia and Australasia. Radiation of tropical and subtropical nectar-feeding vertebrates has occurred throughout most of the Cenozoic in both hemispheres, so hemispheric or regional differences in taxonomic richness and degree of evolutionary specialization cannot be explained solely by different evolutionary ages of nectar-feeding vertebrates. Instead, the geographic patterns we have described ultimately reflect geographic differences in three major factors: (1) the spatio-temporal predictability of floral resources (higher in the Neotropics and Africa than in Southeast Asia and Australasia); (2) the diversity of potentially vertebrate-pollinated flowers (higher in the New World than in the Old World); and (3) the availability of small, hovering birds and bats in the Neotropics but not in the Palaeotropics. While the need to evolve large and sturdy flowers probably limited the evolution of some palaeotropical vertebrate pollination systems, in the Neotropics insect-pollinated plant lineages could more easily switch to bird or bat pollination. This is especially true for relatively small, non-woody plants such as bromeliads and gesneriads. In addition, the evolution of large columnar cacti in arid parts of the Neotropics has favoured an extensive coevolution with nectar-feeding birds and, especially, glossophagine bats (Simmons & Wetterer, 2002; Wallace, 2002). No such coevolution has occurred in arid parts of the Old World. Finally, convergence has clearly occurred in some, but not all, aspects of niche structure in tropical nectar-feeding birds and bats, perhaps most closely in the evolution of hummingbirds and sunbirds. However, significant ecological differences also characterize these two groups (e.g. in their mating systems and degree of gregariousness) as a result of their different phylogenetic histories. In the end, both phylogeny and ecology (e.g. STP of floral resources) have limited the extent to which flower bird and bat niches have converged in the Neotropics and Palaeotropics.

REFERENCES

Aigner, P.A. (2001) Optimality modeling and fitness trade-offs: when should plants become pollinator specialists? *Oikos*, **95**, 177–184.

Altshuler, D.L. & Dudley, R. (2002) The ecological and evolutionary interface of hummingbird flight physiology. *Journal of Experimental Biology*, **205**, 2325–2336.

Altshuler, D.L., Stiles, F.G. & Dudley, R. (2004) Of hummingbirds and helicopters: hovering costs, competitive ability, and foraging strategies. *The American Naturalist*, **163**, 16–25.

Andersen, K. (1912) *Catalogue of the Chiroptera in the collection of the British Museum*, 2nd edn. Trustees of the British Museum (Natural History), London.

Arizmendi, M.C. & Ornelas, J.F. (1990) Hummingbirds and their floral resources in a tropical dry forest in Mexico. *Biotropica*, **22**, 172–180.

Armbruster, W.S. (2006) Evolutionary and ecological aspects of specialized pollination: views from the arctic to the tropics. *Plant–pollinator interactions: from specialization to generalization* (ed. by N.M. Waser and J. Ollerton), pp. 260–282. University of Chicago Press, Chicago, IL.

Armbruster, W.S., Fenster, C.B. & Dudash, M.R. (2000) Pollination 'principles' revisited: specialization, pollination syndromes, and the evolution of flowers. *Det Norske Videnskaps-Akademi. I. Matematiski Naturvidenskapelige Klasse, Skrifter, Ny Serie*, **39**, 179–200.

Baker, H.G. & Harris, B.J. (1957) The pollination of *Parkia* by bats and its attendant evolutionary problems. *Evolution*, **11**, 449–460.

Baker, H.G. & Harris, B.J. (1959) Bat pollination of the silk-cotton tree, *Ceiba pentandra* (L.) Gaertn. (sensu lato) in Ghana. *Journal of the West African Science Association*, **5**, 1–9.

Barker, F.K., Cibois, A., Schikler, P., Feinstein, J. & Cracraft, J. (2004) Phylogeny and diversification of the largest avian radiation. *Proceedings of the National Academy of Sciences USA*, **101**, 1040–1045.

Bawa, K.S. (1990) Plant-pollinator interactions in tropical rain forests. *Annual Review of Ecology and Systematics*, **21**, 399–422.

Benzing, D.H. (2000) *Bromeliaceae, profile of an adaptive radiation*. Cambridge University Press, Cambridge.

Birt, P., Hall, L.S. & Smith, G.C. (1997) Ecomorphology of the tongues of Australian Megachiroptera (Chiroptera: Pteropodidae). *Australian Journal of Zoology*, **45**, 369–384.

Bleiweiss, R. (1998a) Origin of hummingbird faunas. *Biological Journal of the Linnean Society*, **65**, 77–97.

Bleiweiss, R. (1998b) Tempo and mode of hummingbird evolution. *Biological Journal of the Linnean Society*, **65**, 63–76.

Bonaccorso, F.J. (1998) *Bats of Papua New Guinea*. Conservation International, Washington, DC.

Brown, E.D. & Hopkins, M.J.G. (1995) A test of pollinator specificity and morphological convergence between nectarivorous birds and rain-forest tree flowers in New Guinea. *Oecologia*, **103**, 89–100.

Bullock, S.H. (1995) Plant reproduction in neotropical dry forests. *Seasonally dry tropical forests* (ed. by S.H. Bullock, H.A. Mooney and E. Medina), pp. 277–303. Cambridge University Press, Cambridge.

Buzato, S., Sazima, M. & Sazima, I. (2000) Hummingbird-pollinated floras at three Atlantic forest sites. *Biotropica*, **32**, 824–841.

Cheke, R.A. & Mann, C.F. (2001) *Sunbirds: a guide to the sunbirds, flowerpeckers, spiderhunters, and sugarbirds of the world*. Yale University Press, New Haven, CT.

Collinson, M.E., Boulter, M.C. & Holmes, P.L. (1993) Magnoliophyta ('Angiospermae'). *Fossil Record 2* (ed. by M.J. Benton), pp. 809–841. Chapman & Hall, London.

Corlett, R.T. (1998) Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biological Reviews*, **73**, 413–448.

Corlett, R. (2004) Flower visitors and pollination in the Oriental (Indomalayan) region. *Biological Reviews*, **79**, 497–532.

Corlett, R.T. & LaFrankie, J.V. (1998) Potential impacts of climate change on tropical Asian forests through an influence on phenology. *Climatic Change*, **39**, 439–453.

Crepet, W.L. & Friis, E.M. (1987) The evolution of insect pollination in angiosperms. *The origins of angiosperms and their biological consequences* (ed. by E.M. Friis, W.G. Chaloner and P.R. Crane), pp. 181–201. Cambridge University Press, Cambridge.

Crome, F.H.J. & Irvine, A.K. (1986) 'Two bob each way': the pollination and breeding system of the Australian rain forest tree *Syzygium cormiflorum*. *Biotropica*, **18**, 115–125.

Cruden, R.W., Hermann, S.M. & Peterson, S. (1983) Patterns of nectar production and plant-pollinator coevolution. *The biology of nectaries* (ed. by B. Bentley and T. Elias), pp. 80–125. Columbia University Press, New York.

Curran, L.M. & Leighton, M. (2000) Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecological Monographs*, **70**, 101–128.

Davalos, L.M. (2004) *Historical biogeography of the Antilles: Earth history and phylogenetics of endemic chiropteran taxa*. PhD dissertation. Columbia University, New York.

Devy, M.S. & Davidar, P. (2003) Pollination systems of trees in Kakaachi, a mid-elevation wet evergreen forest in Western Ghats, India. *American Journal of Botany*, **90**, 650–657.

Dobat, K. & Peikert-Holle, T. (1985) *Bluten und Fledermause*. Verlag Waldemar Kramer, Frankfurt am Main.

Dowsett-Lemaire, F. (1989) Food plants and the annual cycle in a montane community of sunbirds (*Nectarinia* spp.) in northern Malawi. *Tauraco*, **1**, 167–185.

Dreisig, H. (1997) Why do some nectar foragers perch and others hover while probing flowers? *Evolutionary Ecology*, **11**, 543–555.

Dunning, J.B., Jr ed. (1993) *CRC handbook of avian body masses*. CRC Press, Boca Raton, FL.

Endress, P.K. (1994) *Diversity and evolutionary biology of tropical flowers*. Cambridge University Press, Cambridge.

Faegri, K. & van der Pijl, L. (1979) *The principles of pollination ecology*. Pergamon Press, Oxford.

Feinsinger, P., Swarm, L.A. & Wolfe, J.A. (1985) Nectar-feeding birds on Trinidad and Tobago: comparison of diverse and depauperate guilds. *Ecological Monographs*, **55**, 1–28.

Fenster, C.B., Armbruster, W.S., Wilson, P., Dudash, M.R. & Thomson, J.D. (2004) Pollination syndromes and floral specialization. *Annual Review of Ecology and Systematics*, **35**, 375–403.

Ferrari, S.F. & Strier, K.B. (1992) Exploitation of *Mabea fistulifera* nectar by marmosets (*Callithrix flaviceps*) and muriquis (*Brachyteles arachnoides*) in south-east Brazil. *Journal of Tropical Ecology*, **8**, 225–239.

Fleming, T.H. (2005) The relationship between species richness of vertebrate mutualists and their food plants in tropical and subtropical communities differs among hemispheres. *Oikos*, **111**, 556–562.

Fleming, T.H., Breitwisch, R.L. & Whitesides, G.W. (1987) Patterns of tropical vertebrate frugivore diversity. *Annual Review of Ecology and Systematics*, **18**, 91–109.

Fleming, T.H., Muchhala, N. & Ornelas, J.F. (2005) New World nectar-feeding vertebrates: community patterns and processes. *Contribuciones Mastozoologicas en Homenaje a Bernardo Villa* (ed. by R.A. Medellin and V. Sánchez-Cordero), pp. 161–184. Instituto de Biologia y Instituto de Ecologia, Universidad Nactional Autonoma de Mexico, Mexico.

Ford, H.A., Paton, D.C. & Forde, N. (1979) Birds as pollinators of Australian plants. *New Zealand Journal of Botany*, **17**, 309–319.

Forshaw, J.M. (2006) *Parrots of the world: an identification guide.* Princeton University Press, Princeton, NJ.

Franklin, D.C. & Noske, R.A. (2000) Nectar sources used by birds in monsoonal north-western Australia: a regional survey. *Australian Journal of Botany*, **48**, 461–474.

Freed, L.A., Conant, S. & Fleischer, R.C. (1987) Evolutionary ecology and radiation of Hawaiian passerine birds. *Trends in Ecology & Evolution*, **2**, 196–203.

Freeman, P.W. (1995) Nectarivorous feeding mechanisms in bats. *Biological Journal of the Linnean Society*, **56**, 439–463.

Gentry, A.H. (1982) Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Annals of the Missouri Botanical Garden*, **69**, 557–593.

Giannini, N.P. & Simmons, N.B. (2005) Conflict and congruence in a combined DNA-morphology analysis of megachiropteran bat relationships (Mammalia: Chiroptera: Pteropodidae). *Cladistics*, **21**, 411–437.

Gould, E.H. (1978) Foraging behaviour of Malaysian nectar-feeding bats. *Biotropica*, **10**, 184–193.

Grant, V. (1994) Historical development of ornithophily in the western North American flora. *Proceedings of the National Academy of Sciences USA*, **91**, 10,407–10,411.

Heithaus, E.R., Opler, P.A. & Baker, H.G. (1974) Bat activity and pollination of *Bauhinia pauletia*: plant–pollinator coevolution. *Ecology*, **55**, 412–419.

Heithaus, E.R., Fleming, T.H. & Opler, P.A. (1975) Patterns of foraging and resource utilization in seven species of bats in a seasonal tropical forest. *Ecology*, **56**, 841–854.

von Helversen, O. (1993) Adaptations of flowers to the pollination by glossophagine bats. *Plant–animal interactions in tropical environments* (ed. by W. Barthlott, C.M. Naumann, K. Schmidt-Loske and K. Schuchmann), pp. 41–59. Museum Alexander Koenig, Bonn, Germany.

von Helversen, O. & Winter, Y. (2003) Glossophagine bats and their flowers: cost and benefit for flower and pollinator. *Bat ecology* (ed. by T.H. Kunz and M.B. Fenton), pp. 346–397. University of Chicago Press, Chicago.

Heywood, V.H. ed. (1993) *Flowering plants of the world.* Oxford University Press, New York.

Irwin, M.P.S. (1999) The genus *Nectarinia* and the evolution of sunbirds: an Afrotropical perspective. *Honeyguide*, **45**, 45–58.

Itino, T., Kato, M. & Hotta, M. (1991) Pollination ecology of the two wild bananas, *Musa acuminata* subsp. *halabanensis* and *M. salaccensis*: chiropterophily and ornithophily. *Biotropica*, **23**, 151–158.

Janson, C.H., Terborgh, J. & Emmons, L. (1981) Non-flying mammals as pollination agents in the Amazonian forest. *Biotropica*, **13**, 1–6.

Johnson, S.D. & Brown, M. (2004) Transfer of pollinaria on birds' feet: a new pollination system in orchids. *Plant Systematics and Evolution*, **244**, 181–188.

Johnson, S.D. & Steiner, K.E. (2000) Generalization versus specialization in plant pollination systems. *Trends in Ecology & Evolution*, **15**, 140–143.

Jones, K.E., Bininda-Emonds, O.R.P. & Gittleman, J.L. (2005) Bats, clocks, and rocks: diversification patterns in Chiroptera. *Evolution*, **59**, 2243–2255.

Kirsch, J.A.W., Flannery, T.F., Springer, M.S. & Lapointe, F.J. (1995) Phylogeny of the Pteropodidae (Mammalia, Chiroptera) based on DNA hybridization, with evidence for bat monophyly. *Australian Journal of Zoology*, **43**, 395–428.

Kitchener, D.J., Gunnell, A. & Maharadatunkamsi (1990) Aspects of the feeding biology of fruit bats (Pteropodidae) on Lombok Island, Nusa Tenggara, Indonesia. *Mammalia*, **54**, 561–578.

Kress, W.J. (1985) Bat pollination of an Old-World *Heliconia*. *Biotropica*, **17**, 302–308.

Kress, W.J. & Beach, J.H. (1994) Flowering plant reproductive systems. *La Selva, ecology and natural history of a neotropical rain forest* (ed. by L.A. McDade, K.S. Bawa, H.A. Hespenheide and G.S. Hartshorn), pp. 161–182. University of Chicago Press, Chicago.

Law, B.S. & Lean, M. (1999) Common blossom bats (*Syconycteris australis*) as pollinators in fragmented Australian tropical rain forest. *Biological Conservation*, **91**, 201–212.

Lovette, I.J., Bermingham, E. & Ricklefs, R.E. (2001) Clade-specific morphological diversification and adaptive radiation in Hawaiian songbirds. *Proceedings of the Royal Society B: Biological Sciences*, **269**, 37–42.

Marshall, A.G. & McWilliam, A.N. (1982) Ecological observations on epomophorine fruit-bats (Megachiroptera) in West African savanna woodland. *Journal of Zoology, London*, **198**, 53–67.

Mayr, G. (2004) Old World fossil record of modern-type hummingbirds. *Science*, **304**, 861–864.

Mayr, G. (2005) Fossil hummingbirds in the Old World. *Biologist*, **52,** 12–16.

Mayr, G. (2007) New specimens of the early Oligocene old world hummingbird *Eurotrochilus inexpectatus*. *Journal of Ornithology*, **148,** 105–111.

Mickleburgh, S.P., Hutson, A.M. & Racey, P.A. eds (1992) *Old World fruit bats, an action plan for their conservation*. International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland.

Muchhala, N. (2006a) Nectar bat stows huge tongue in its rib cage. *Nature*, **444,** 701–702.

Muchhala, N. (2006b) The pollination biology of *Burmeistera* (Campanulaceae): specialization and syndromes. *American Journal of Botany*, **93,** 1081–1089.

Muchhala, N. & Jarrín, V.-P. (2002) Flower visitation by bats in cloud forests of western Ecuador. *Biotropica*, **34,** 387–395.

Muscarella, R. & Fleming, T.H. (2007) The role of frugivorous bats in tropical forest succession. *Biological Reviews*, **82,** 573–590.

Nicolson, S.W. & Fleming, P.A. (2003) Nectar as food for birds: the physiological consequences of drinking dilute sugar solutions. *Plant Systematics and Evolution*, **238,** 139–153.

Noske, R.A. (1995) The ecology of mangrove forest birds in peninsular Malaysia. *Ibis*, **137,** 250–263.

Nowak, R.M. (1994) *Walker's bats of the world*. Johns Hopkins University Press, Baltimore, MD.

Ollerton, J., Johnson, S.D. & Hingston, A.B. (2006) Geographical variation in diversity and specificity of pollination systems. *Plant–pollinator interactions: from specialization to generalization* (ed. by N.M. Waser and J. Ollerton), pp. 283–308. University of Chicago Press, Chicago.

Ollerton, J., Killick, A., Lamborn, E., Watts, S. & Whiston, M. (2007) Multiple meanings and modes: on the many ways to be a generalist flower. *Taxon*, **56,** 717–728.

Opler, P.A. (1983) Nectar production in a tropical ecosystem. *The biology of nectaries* (ed. by B. Bentley and T. Elias), pp. 30–79. Columbia University Press, New York.

Palmer, C., Price, O. & Bach, C. (2000) Foraging ecology of the black flying fox (*Pteropus alecto*) in the seasonal tropics of the Northern Territory. *Australian Wildlife Research*, **27,** 169–178.

Paton, D.C. (1986) Honeyeaters and their plants in southeastern Australia. *The dynamic partnership: birds and plants in southern Australia* (ed. by H.A. Ford and D.C. Paton), pp. 9–19. Government of South Australia, Adelaide.

Paton, D.C. & Ford, H.A. (1977) Pollination by birds of native plants in Australia. *Emu*, **77,** 73–85.

Pauw, A. (1998) Pollen transfer on birds' tongues. *Nature*, **394,** 731–732.

Pellmyr, O. (2002) Pollination by animals. *Plant–animal interactions: an evolutionary approach* (ed. by C.M. Herrera and O. Pellmyr), pp. 157–184. Blackwell Science Ltd, Oxford.

Pettet, A. (1977) Seasonal changes in nectar feeding by birds at Zaria, Nigeria. *Ibis*, **119,** 291–308.

Primack, R. & Corlett, R. (2005) *Tropical rain forests: an ecological and biogeographical comparison*. Blackwell Science Ltd, Malden, MA.

Proctor, M., Yeo, P. & Lack, A. (1996) *The natural history of pollination*. Timber Press, Portland.

Pyke, G.H. (1980) The foraging behaviour of Australian honeyeaters: a review and some comparisons with hummingbirds. *Australian Journal of Ecology*, **5,** 343–369.

Rand, A.L. & Gilliard, E.T. (1967) *Handbook of New Guinea birds*. Weidenfeld and Nicolson, London.

Rebelo, A.G. (1987) Bird pollination in the Cape flora. *South African National Science Progress Report*, **141,** 83–108.

Regal, P.J. (1982) Pollination by wind and animals: ecology of geographic patterns. *Annual Review of Ecology and Systematics*, **13,** 497–524.

Richards, G.C. (1995) A review of ecological interactions of fruit bats in Australian ecosystems. *Ecology, evolution and behaviour of bats* (ed. by P.A. Racey and S. Swift), pp. 79–96. Clarendon Press, Oxford.

Sakai, S. (2000) Reproductive phenology of gingers in a lowland mixed dipterocarp forest in Borneo. *Journal of Tropical Ecology*, **16,** 337–354.

Sakai, S. (2001) Phenological diversity in tropical forests. *Population Ecology*, **43,** 77–86.

Sazima, M., Buzato, S. & Sazima, I. (1999) Bat-pollinated flower assemblages and bat visitors at two Atlantic forest sites in Brazil. *Annals of Botany*, **83,** 705–712.

Sazima, M. & Sazima, I. (1975) Quiropterofilia em *Lafoensia pacari* St. Hil. (Lythraceae), na Serra do Cipo, Minas Gerais. *Ciencia e Cultura*, **27,** 405–416.

Schuchmann, K.L. (1999) Family Trochilidae (hummingbirds). *Handbook of the birds of the world*, Vol. 5 (ed. by J. del Hoyo, A. Elliot and J. Sargatal), pp. 468–680. Lynx Editions, Barcelona.

Sekercioglu, C.H. (2006) Increasing awareness of avian ecological function. *Trends in Ecology & Evolution*, **21,** 464–471.

Sibley, C.G. & Monroe, B.L. (1990) *Distribution and taxonomy of birds of the world*. Yale University Press, London.

Simmons, N.B. (2005) Order Chiroptera. *Mammal species of the world, a taxonomic and geographic reference* (ed. by D.E. Wilson and D.M. Reeder), pp. 312–529. Johns Hopkins Press, Baltimore, MD.

Simmons, N.B. & Voss, R.S. (1998) The mammals of Paracou, French Guiana: a neotropical lowland rain forest fauna. Part I. Bats. *Bulletin of the American Museum of Natural History*, Number 237. New York.

Simmons, N.B. & Wetterer, A.L. (2002) Phylogeny and convergence in cactophilic bats. *Columnar cacti and their mutualists: evolution, ecology, and conservation* (ed. by T.H. Fleming and A. Valiente-Banuet), pp. 87–121. University of Arizona Press, Tucson, AZ.

Snow, B.K. & Snow, D.W. (1972) Feeding niches of hummingbirds in a Trinidad valley. *Journal of Animal Ecology*, **41,** 471–485.

Snow, D.W. & Snow, B.K. (1980) Relationships between hummingbirds and flowers in the Andes of Colombia. *Bulletin of the British Museum of Natural History (Zoology)*, **38**, 105–139.

Start, A.N. & Marshall, A.G. (1976) Nectarivorous bats as pollinators of trees in West Malaysia. *Tropical trees, variation, breeding, and conservation* (ed. by J. Burley and B.T. Styles), pp. 141–150. Academic Press, London.

Stiles, F.G. (1977) Co-adapted competitors: the flowering seasons of hummingbird-pollinated plants in a tropical forest. *Science*, **196**, 1177–1178.

Stiles, F.G. (1981) Geographical aspects of bird–flower coevolution, with particular reference to Central America. *Annals of the Missouri Botanical Gardens*, **68**, 323–351.

Stiles, F.G. (2004) Phylogenetic constraints upon morphological and ecological adaptation in hummingbirds (Trochilidae): why are there no hermits in the paramo? *Ornitologia Neotropical*, **15**, 191–198.

Stiles, F.G., Altshuler, D.L. & Dudley, R. (2005) Wing morphology and flight behaviour of some North American hummingbird species. *The Auk*, **122**, 872–886.

Stockwell, E.F. (2001) Morphology and flight manoeuvrability in New World leaf-nosed bats (Chiroptera: Phyllostomidae). *Journal of Zoology*, **254**, 505–514.

Swanepoel, P. & Genoways, H.H. (1979) Morphometrics. *Biology of bats of the New World family Phyllostomatidae, Part 3* (ed. by R.J. Baker, J.K. Jones Jr and D.C. Carter), pp. 13–106. Special Publications of the Museum, Texas Tech University, Lubbock, TX.

Tarr, C.L. & Fleischer, R.C. (1995) Evolutionary relationships of the Hawaiian honeycreepers (Aves, Drepanidinae). *Hawaiian biogeography* (ed. by W.L. Wagner and V.A. Funk), pp. 147–159. Smithsonian Institution Press, Washington, DC.

Teeling, E.C., Springer, M.S., Madsen, O., Bates, P., O'Brien, S.J. & Murphy, W.J. (2005) A molecular phylogeny for bats illuminates biogeography and the fossil record. *Science*, **307**, 580–584.

Temeles, E.J. & Kress, W.J. (2003) Adaptation in a plant–hummingbird association. *Science*, **300**, 630–633.

Tschapka, M. & von Helversen, O. (1999) Pollinators of syntopic *Marcgravia* species in Costa Rican lowland rain forest: bats and opossums. *Plant Biology*, **1**, 382–388.

van Schaik, C.P. & Pfannes, K.R. (2005) Tropical climates and phenology: a primate perspective. *Seasonality in primates: studies of living and extinct human and non-human primates* (ed. by D.K. Brockman and C.P. van Schaik), pp. 23–54. Cambridge University Press, Cambridge.

Vardon, M.J., Brocklehurst, P.S., Woinarski, J.C.Z., Cunningham, R.B., Donnelly, C.F. & Tidemann, C.R. (2001) Seasonal habitat use by flying-foxes, *Pteropus alecto* and *P. scapulatus* (Megachiroptera), in monsoonal Australia. *Journal of Zoology*, **253**, 523–535.

Wallace, R.S. (2002) The phylogeny and systematics of columnar cacti: an overview. *Columnar cacti and their mutualists: evolution, ecology, and conservation* (ed. by T.H. Fleming and A. Valiente-Banuet), pp. 42–65. University of Arizona Press, Tucson, AZ.

Waser, N.M., Chittka, L., Price, M.V., Williams, N.M. & Ollerton, J. (1996) Generalization in pollination systems, and why it matters. *Ecology*, **77**, 1043–1060.

Westerkamp, C. (1990) Bird-flowers: hovering versus perching exploitation. *Botanica Acta*, **103**, 366–371.

Whitmore, T.C. (1998) *An introduction to tropical rain forests*, 2nd edn. Clarendon Press, Oxford.

Wilson, P., Castellanos, M.C., Wolfe, A.D. & Thomson, J.D. (2006) Shifts between bee and bird pollination in penstemons. *Plant–pollinator interactions* (ed. by N.M. Waser and J. Ollerton), pp. 47–68. University of Chicago Press, Chicago, IL.

Woinarski, J.C.Z., Franklin, D. & Connors, G. (2000) Thinking honeyeater: nectar maps for the Northern Territory, Australia, showing spatial and temporal variation in nectar availability. *Pacific Conservation Biology*, **6**, 61–80.

Wolf, L.L., Stiles, F.G. & Hainsworth, F.R. (1976) Ecological organisation of a tropical, highland hummingbird community. *Journal of Animal Ecology*, **45**, 349–380.

Woodside, D. & Pyke, G.H. (1985) A comparison of bats and birds as pollinators of *Banksia integrifolia* in northern New South Wales. *Australian Mammalogy*, **18**, 9–18.

Wright, D.D. (1998) *Fruit choice by the dwarf cassowary, Casuarius bennetti, over a three year period in Papua New Guinea*. PhD thesis. University of Miami, Miami, FL.

Yumoto, T. (2005) Vertebrate-pollinated plants. *Pollination ecology and the rain forest* (ed. by D.W. Roubik, S. Sakai and A.A.H. Karim), pp. 134–144. Springer, New York.

Yumoto, T., Itino, T. & Nagamasu, H. (1997) Pollination of hemiparasites (Loranthaceae) by spider hunters (Nectariniidae) in the canopy of a Bornean rain forest. *Selbyana*, **18**, 51–60.

Ziegler, A.C. (2002) *Hawaiian natural history, ecology, and evolution*. University of Hawai'i Press, Honolulu, HI.

BIOSKETCHES

Theodore Fleming has studied tropical plant–animal interactions, primarily in the New World, for over three decades. His main focus has been on bat–plant interactions involving both seed dispersal and pollination. Habitats he has worked in include tropical rain forest, tropical dry forest, and the Sonoran Desert. His field sites have been in Panama, Costa Rica, Mexico, Arizona, and Australia.

Nathan Muchhala has just completed his doctoral studies on the evolution of pollinator specialization in the plant genus *Burmeistera* (Campanulaceae). His field studies were conducted in the mountains of Costa Rica and Ecuador.

Editor: Lawrence Heaney