

Behavioural environments and niche construction: the evolution of dim-light foraging in bees

William T. Wcislo* and Simon M. Tierney

Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, Republic of Panamá

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ABSTRACT

Most bees forage for floral resources during the day, but temporal patterns of foraging activity vary extensively, and foraging in dim-light environments has evolved repeatedly. Facultative dim-light foraging behaviour is known in five of nine families of bees, while obligate behaviour is known in four families and evolved independently at least 19 times. The light intensity under which bees forage varies by a factor of 10^8 , and therefore the evolution of dim-light foraging represents the invasion of a new, extreme niche. The repeated evolution of dim-light foraging behaviour in bees allows tests of the hypothesis that behaviour acts as an evolutionary pacemaker. With the exception of one species of *Apis*, facultative dim-light foragers show no external structural traits that are thought to enable visually mediated flight behaviour in low-light environments. By contrast, most obligate dim-light foragers show a suite of convergent optical traits such as enlarged ocelli and compound eyes. In one intensively studied species (*Megalopta genalis*) these optical changes are associated with neurobiological changes to enhance photon capture. The available ecological evidence suggests that an escape from competition for pollen and nectar resources and avoidance of natural enemies are driving factors in the evolution of obligate dim-light foraging.

Key words: foraging behavior, nocturnal, crepuscular, matinal, vespertine, evolution, niche shifts, niche construction, neurobiology of night vision, Apoidea.

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* Address for correspondence (E-mail: WcisloW@si.edu).

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I. INTRODUCTION

Bees are generally regarded as sun-loving creatures (Michener, 2007). Indeed, most bees fly under full sun but some have evolved an ability to fly in very dim light conditions—including moonlight and even starlight—and so bees of different species experience foraging environments in which average light intensity varies by a factor of more than 10^8 (i.e. the difference between sunlight and starlight; see Lythgoe, 1979; Warrant, 2004). Thus, for day-flying species the evolution of dim-light foraging represents the invasion of an extreme environment, and provides an opportunity to look at the relative roles of behavioural, physiological, and structural changes in facilitating these niche shifts.

Mayr (1960, p. 371) argued that the invasion of a new niche invariably establishes a new array of selection pressures, and that such shifts require “almost without exception” a change in behaviour. Changes in behaviour may then lead to subsequent evolutionary changes in other features favourable for life in the new environment, although they are not inevitable (e.g. Darwin, 1872; Mayr, 1958; Evans, 1966; Wcislo, 1989; Prum, 1998; Odling-Smee, Laland & Feldman, 2003; West-Eberhard, 2003). The hypothesis that behaviour shapes selective environments, and acts as a pacemaker of evolution, dates to Lamarck (1809) and subsequent Darwinian formulations by Baldwin (1902) and others (see reviews in Lewontin, 1983, 2000; Wcislo, 1989; West-Eberhard, 2003; Odling-Smee *et al.*, 2003; Weber & Depew, 2003). Odling-Smee *et al.* (2003) review methods to test for the relative importance of organism-induced modifications of their selective environment, which they termed “niche construction” (following Lewontin, 2000). One test involves comparative methods: if facultative behaviour takes the lead in initiating evolutionary change, then the distribution of character states across a phylogeny should reveal that traits associated with the new environment are concentrated in those branches of the tree where the novel (niche constructing) behaviour is obligatory (*cf.* Fig. 1 of Wcislo, 1989).

Here we first review the phyletic distribution of dim-light foraging in bees, both facultative and obligate, as well as the phenotypic traits that enable such activity. We then use these comparative data to test the relative importance of temporal niche construction in shaping the evolution of foraging patterns of bees, and the structural and physiological traits associated with the novel behaviour.

II. METHODS

(1) Ethological comparisons

Data on dim-light foraging behaviour were taken from the ethological literature. Published reports vary in the extent to which they present quantitative data on foraging times, and few present quantitative data on light levels (see Roberts, 1971; Burgett & Sukumalanand, 2000; Kelber *et al.*, 2006; Somanathan *et al.*, 2008). Naturalists have traditionally used categories corresponding to varying light levels to classify dim-light foraging in bees (summarised by Linsley & Cazier, 1970). For our purposes, we consider species as being: matinal- if authors specified that bees were active before sunrise; vespertine- if bees are active in post-sunset twilight; crepuscular- if bees are active during both of the above periods; and nocturnal- if they are active between evening and morning twilight. Collectively we refer to these taxa as dim-light bees. References to activity around twilight periods are often ambiguous because most authors do not specify whether they refer to civil, nautical or astronomical twilight; presumably most naturalists used an approximation to civil twilight as assessed by their own eyes. Furthermore, categorical classifications alone may not accurately reflect light levels experienced by the bees. For example, due to both latitude and plant canopy architecture, a bee active at sunrise/sunset in a temperate desert will experience strikingly different light levels than one active at the same times in a tropical evergreen forest (e.g. Kelber *et al.*, 2006), or a tropical dry forest, even though all would be categorized as crepuscular. Furthermore, some bees [e.g., *Lasioglossum (Sphecodogastra) texanum* (Halictidae)] are usually crepuscular, but will extend their evening activity later into the night when reflectance from the moon is bright (Kerfoot, 1967a; also Somanathan *et al.*, 2008).

(2) Phylogenetic comparisons

The dearth of relevant phylogenetic hypotheses is an impediment to detailed species-level comparisons among dim-light taxa. The halictid tribe Augochlorini is the taxon with the greatest diversity of dim-light foragers for which phylogenetic data are available (Eickwort, 1969; Engel, 2000; see Wcislo *et al.*, 2004). We used Engel's (2000) consensus phylogenetic hypothesis for the Augochlorini, with the modifications described below. This tree includes 39 genera and subgenera, and is based on 72 anatomical characters and 12 behavioural characters. Rather than

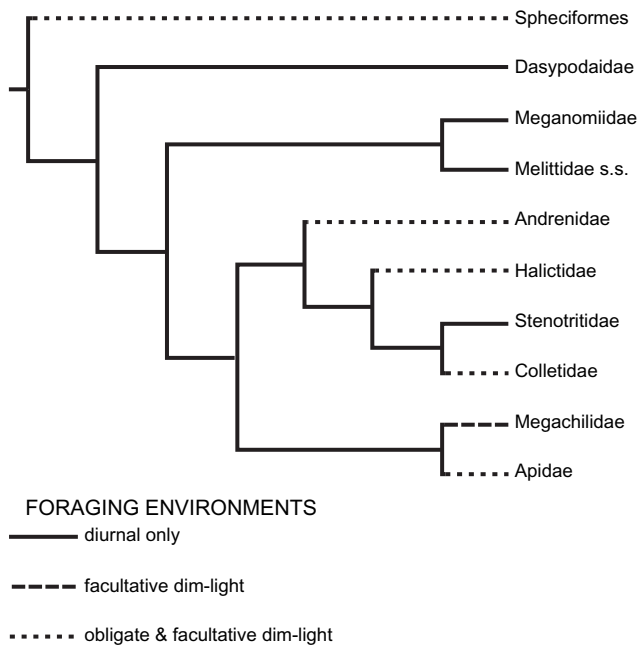


Fig. 1. Cladogram of the families of bees (Apoidea) (adapted from Michener, 2007, p. 92), with the phyletic distribution of facultative and obligate dim-light taxa.

using species as terminal taxa, we used genera and subgenera. Maddison's test for concentrated changes does not allow for polytomies, so the several polytomies in the tree were randomly resolved as bifurcating trees. Maddison (1990) discusses several assumptions that are unlikely to be met in this analysis (see also Read & Nee, 1995).

Consequently, a second analysis was performed by first identifying a putative or hypothesised sister taxon for each taxon with dim-light foragers. Effectively this sets up a matched-pairs comparison, with one sister taxon showing the focal trait (i.e. dim-light foraging) and the other taxon not expressing this trait (i.e. diurnal foraging) (Read & Nee, 1995).

(3) Relative body size

Body size of dim-light bees relative to diurnal ones was examined using the 169 genera of Central and North America, which Michener, McGinley & Danforth (1994, pp. 125–172) classified as ranging within five categories (minute, small, moderate, large, very large). Taxa with body sizes that ranged across more than one category (e.g. minute to moderate) were counted in each one. We then broadly classified the foraging habits of each genus as 'diurnal', 'facultative dim-light', or 'obligate dim-light'. This typology is problematic due to the occurrence of genera that contain both diurnal and dim-light species, so the following caveats apply. First, we considered a genus to be 'dim-light' if it contained at least one dim-light foraging species, and if a dim-light genus contained both facultative and obligate dim-light foraging species, we considered it to be an 'obligate' dim-light clade. Furthermore, a genus was categorised as 'facultative' or 'obligate' only if dim-light

foraging members of the clade exist in the region covered by Michener *et al.*'s (1994) monograph. For example, in *Megommation* the subgenera *M. (Cleptommation)* and *M. (Megaloptina)* are distributed in Panamá and Costa Rica, but the sole dim-light species, *M. (Megommation) insigne* Smith, is restricted to the southeastern tropics of South America, and thus for our analysis Central and North American *Megommation* s.l. are categorised as diurnal.

III. OVERVIEW OF DIM-LIGHT FORAGING IN BEES

(1) Facultative dim-light foraging

The true frequency of facultative dim-light foraging is unknown, because most bee biologists, like most bees, are active during the day, and numerous species have never been studied in any detail (Michener, 2007). Facultative dim-light foraging occurs in species representing nearly all the major lineages (Fig. 1, Table 1). Diurnal bees, such as some carpenter bees (*Xylocopa* spp.), can be heard flying in the pre-dawn darkness, collecting pollen from diurnal flowers with early anthesis, and have been collected at light traps (Rau, 1933; Hurd, 1958; Wolda & Roubik, 1986). *X. (Mesotrichia) tenuiscapa* Westwood is primarily diurnal and seasonally switches to crepuscular foraging (Somanathan & Borges, 2001; Somanathan *et al.*, 2008). Temporal versatility with respect to foraging is known for several species of halictine bees: *Agapostemon angelicus* Cockerell, for example, regularly uses pollen or nectar from diurnal flowers, but also collects resources from plants before sunrise or around sunset (Linsley, 1960; see Roberts, 1969, 1972). Female foragers of the Old World honey bee (*Apis dorsata* Fabricius) are normally day-active, yet continue foraging into the night during a half to full moon (Dyer, 1985). Males of this species consistently fly at dusk for mating flights (see Section III. 1a). Conversely, in the deserts of the southern USA, *Martinapis occidentalis* Zavortink & La Berge (= *luteicornis* of Hurd & Linsley, 1975), for example, collects pollen at dawn from creosote bush (*Larrea tridentata*) and palo verde (*Parkinsonia florida*), but also has been recorded collecting pollen during the day (see Linsley & Hurd, 1959; Zavortink & LaBerge, 1976). Of the estimated 187 species of bees on Barro Colorado Island (Panamá) catalogued by Michener (1954), 45 diurnal species have been collected at black light traps, suggesting facultative dim-light foraging behaviour (Wolda & Roubik, 1986). Many of these species are stingless bees (Meliponini), which often begin foraging before sunrise and collect the dregs of pollen that remain on night-blooming plants (Roubik 1989; Wolda & Roubik 1986), but some stingless bees have also been collected at lights during a full moon (post-vespertine) in northwestern Panamá (S. M. Tierney, personal observation).

(a) Phenotypic changes associated with facultative dim-light foraging

In all but one case, there are no evident external features of the visual system that are associated with a facultative

Table 1. List of known dim-light-foraging bees, categorised according to flight times: D = diurnal; N = nocturnal; C = crepuscular (both matinal and vespertine); M = matinal; V = vespertine; LT = collected at light trap at night and no data on foraging times are available; P = parasitic, and females search for host nests rather than flowers. Obligate taxa are highlighted in bold. Large body size may be associated with obligate dim-light foraging (see section III. 2aii), but this trait is not included here under 'Anatomical features for dim-light behaviour'. Distributional information was taken from Michener (2007) and an electronic compilation by J. S. Ascher (http://www.discoverlife.org/mp/20q?act=x_giode_credit&guide=Apoidea_species)

Dim-light taxa (taxa with obligate dim-light species in bold)	<i>N. species</i>	Temporal patterns	Anatomical features for dim-light behaviour	Closest diurnal relative	References
ANDRENIDAE					
Andreninae					
<i>Andrena</i> (<i>Onagrاندrena</i>)	24	M	none	<i>A. (Melanapis) + A. (Rhapاندrena) or A. (Troاندrena)</i>	Linsley <i>et al.</i> (1964); Dubitzky (2005)
(<i>Diاندrena</i>)	2	M	none	<i>A. (Scoliاندrena)</i>	LaBerge & Hurd (1965); Thorp (1969); Dubitzky (2005)
Panurginae					
<i>Pendula</i> (<i>Xerophاسma</i>)	2	LT	enlarged ocelli & compound eyes	<i>P. (Allopendita)</i>	Cockerell (1923); Danforth (1991)
Oxaeinae					
<i>Protoxaeا gloriosa</i>	1	M - visits <i>Solanum</i> spp. ~"15 minutes before sunrise"	none	<i>Mesoxaea</i>	Linsley & Cazier (1972)
HALICTIDAE					
Halictinae					
<i>Lasiglossum</i> L. (<i>Dialictus</i>)	at least 1	N	none	other <i>Dialictus</i>	D. Yanega (personal communication)
L. (<i>Sphecodogastra</i>)	8	C; regularly collected at light traps; one species extends activity at night under full or waxing moon	Two species with enlarged ocelli; six with normal or slightly enlarged ocelli	<i>L. (Epylaeus)</i>	Graenicher (1911); Stevens (1920); Chandler (1961); Knerer & MacKay (1969); Bohart & Youssef (1976); Kelber <i>et al.</i> (2006); Kerfoot (1967a,b); McGinley (2003)
L. (<i>Hemihalictus</i>) lustrans	1	M - specialist on <i>Pyrrhophaps</i> and begins foraging at dawn	none	<i>L. (Epylaeus) pectorale</i>	Michener (1947); Daly (1961); Estes & Thorp (1975); Danforth <i>et al.</i> (2003a)
<i>Mexalictus</i>	at least 1	N	none	other <i>Mexalictus</i>	D. Yanega (personal communication)
<i>Rhinetula dentricus</i>	1	LT	none	<i>Dinagapostemon</i>	Janzen (1968); Wolda & Roubik (1986); Roberts & Brooks (1987)

Augochlorini	Megalopta s. str.	~ 27	C, some possibly N	enlarged ocelli; enlarged ommatidia; neural rewiring and neuro-physiological changes	<i>Xenochlora</i>	Ducke (1902); Schwarz (1934); Linsley <i>et al.</i> (1963); Wolda & Roubik (1986); Listabarth (1996); Roulston (1997); Engel (2000); Smith & Knapp (2002); Wcislo <i>et al.</i> (2004); Kelber <i>et al.</i> (2006); Warrant <i>et al.</i> (2004); Tierney <i>et al.</i> (2008a)
	M. (Noctoraptor) P	3	C	enlarged ocelli and compound eyes	<i>Xenochlora</i>	Engel <i>et al.</i> (1997); Biani & Wcislo (2007)
	Megaloptidia	3	presumably N or C	enlarged ocelli and compound eyes	<i>Micrommatina and Aphanarctia</i>	Cockerell (1900); Moure (1958); Eickwort (1969); Engel & Brooks (1998); Engel (2000)
	Megommation insigne	1	presumably N or C	enlarged ocelli and compound eyes	<i>Megaloptina</i>	Jørgensen (1912); Michener & Lange (1958); Sakagami & Moure (1967); Eickwort (1969); Engel (2000)
	<i>Augochlora</i> sp.	1	LT	none	other <i>Augochlora</i>	Wolda & Roubik (1986)
COLLETIDAE	Caupolicana s. s.	42	most species C or M; D—e.g. <i>C. notabilis</i> was collected near mid-day (A. Wetmore, cited in Michener, 1966); <i>C. (Caupolicana) ocellata</i> may extend activity into N (P. H. Raven, cited in Michener 1966)	<i>C. (Caupolicana) ocellata</i> has enlarged ocelli	(<i>Crucifordapis</i> + <i>Ptiloglossa</i>)	Cockerell & Porter (1899); Graenicher (1930); Linsley & Cazier (1970, 1972); Michener (1966); Rozen (1984)
	Ptiloglossa	~40	considerable variation: some species are early M (e.g. <i>P. arizonensis</i>); others fly both in early morning and evening (e.g. <i>P. guinnae</i> , <i>P. eximia</i>); others may be N (e.g. <i>P. fulvopilosa</i>)	<i>Ptiloglossa</i> sp. from Argentina with enlarged ocelli	<i>Crucifordapis</i>	Schrottky (1907); Veseý-FitzGerald (1939); Linsley (1962); Linsley & Cazier (1970, 1972); Roberts (1971); Rozen (1984); D. Yanega (personal communication)
Diphaglossini	Dissoglotini	11	most species are rare and behaviourally unknown; <i>Myrdrosoma</i> sp. visits flowers in late afternoon	none		Michener (1986)
Colletinae	Colletes stephensi	1	M- predawn flights that continue to 1.5 h post sunrise	none	other <i>Colletes</i>	Hurd & Powell (1958); Hurd & Linsley (1975)
MEGACHILIDAE	<i>Megachile</i> spp.	2	LT	none	other <i>Megachile</i>	Wolda & Roubik (1986)
APIDAE						

Table 1. (cont.)

Dim-light taxa (taxa with obligate dim-light species in bold)	<i>N</i> species	Temporal patterns	Anatomical features for dim-light behaviour	Closest diurnal relative	References
Apinae Apini	1	D, LT		other <i>A. mellifera</i> sub-species	Wolda & Roubik (1986)
	1	D, C; N under half to full moon	ocelli on raised vertex that is pronounced in males	<i>A. laboriosa</i>	Dyer (1985); Momose <i>et al.</i> (1998)
Bombini	1	D, M-active "15 minutes before sunrise"	none	other <i>Bombus</i>	Linsley & Cazier (1972)
Centridini	4	LT	none	other <i>Centris</i>	Wolda & Roubik (1986)
	2	LT	none	other <i>Epicharis</i>	Wolda & Roubik (1986)
Ericrocidini	1	LT	none	other <i>Mesoplia</i>	Wolda & Roubik (1986)
Eucerini	7	M; before dawn	enlarged ocelli	<i>Xenoglossa (Eoxenoglossa)/ Peponapis</i>	Linsley <i>et al.</i> (1956); Hurd & Linsley (1964, 1967; 1970)
	1	M?	enlarged ocelli	other Eucerini	LaBerge (1992)
	2	D, C	none	<i>Simantheodon</i>	Hurd & Linsley (1975); Zavortink & LaBerge (1976)
	1	possibly C, and D	none	other <i>Martinapis</i>	Zavortink & LaBerge (1976)
	1	LT	none	other <i>Melissophila</i>	Wolda & Roubik (1986)
	13	M	none	Eucerini	Hurd & Linsley (1970)
<i>Tetralonia speciosa</i>	1	M - before dawn	none	other Tetralonia	Bohart & MacSwain, cited in Bohart & Youssef (1976)
Epeolini		P - presumably C or N	enlarged ocelli	<i>Odyneropsis</i> (<i>Parannobates</i>) + <i>Rhagepeolus</i>	F. Bennett, cited in Rozen (1966); Rozen (1984)
Meliponini	3	LT	none	other <i>Melipona</i>	Wolda & Roubik (1986)
	24	LT	none	other <i>Trigona</i>	Wolda & Roubik (1986)
	1	LT	none	other <i>Lestrimelitta</i>	Wolda & Roubik (1986)
Tapinotaspidini	2	LT	none	other <i>Paratetrapedia</i>	Wolda & Roubik (1986)
Nomadinae	>1	D, M - cleptoparasites of <i>Onagraderma</i>	none	other nomadines	D. Yanega (personal communication)
Xylocopinae		D, M in summer	none	<i>Xylocopa</i> s.s.	Gerling <i>et al.</i> (1983)
	1	D, M in summer	none	<i>Mesotrichia</i>	Gerling <i>et al.</i> (1983)
	1	D, C	none	Subgenus	Somanathan & Borges (2001); Somanathan <i>et al.</i> (2006, 2008)
	1	C	none	<i>Hoploxylocopa</i> sister group to remaining American <i>Xylocopa</i>	Janzen (1964); Hurd & Linsley (1975); Barthell & Knops (1997)
<i>X. (Nyctomelitta)</i>	3	N	enlarged compound eyes and ocelli		Bingham (1897); Burgett & Sukumalanand (2000); Somanathan <i>et al.</i> (2004, 2008)
<i>X. (Proxylocopa)</i>	1+	C or N	some species with enlarged ocelli	American subgenera	Gottlieb <i>et al.</i> (2005)

ability to forage under dim-light conditions, suggesting that the move into the new temporal environment is a behavioural response to exploit new resources. *Apis dorsata* Linnaeus have a raised vertex so that ocelli are more pronounced, and this trait is more noticeable in drones than workers, which is hypothesised to be related to mating flights that are consistently restricted to a very brief vespertine window (Koeniger *et al.*, 1994; Otis, 1996; Koeniger & Koeniger, 2000). Ocellar size of *A. dorsata*, however, is not proportionally larger than their closest diurnal relative, *A. laboriosa* Smith (Maa, 1953; Sakagami, Matsumura & Itô, 1980). We lack detailed studies on the sensory ecology of facultative dim-light foragers, and therefore it is possible that there are slight differences in ocular or ommatidial size, and neuroanatomy or neurophysiology that might promote facultative dim-light foraging. Warrant, Porombka & Kirchner (1996), for example, suggest that neural processing at a higher level enables photon summation in honey bees (*Apis*), which enables foraging activity under dim light. Both among and within species, bees with larger bodies have larger compound eyes with larger ommatidia, and thus can fly at lower light levels (Jander & Jander, 2002; Spaethe & Chittka, 2003; Kelber *et al.*, 2006; Kapustjanskij *et al.*, 2007; Somanathan *et al.*, 2008). Large body size therefore might be a pre-adaptation to the evolution of dim-light foraging because the larger facet diameter will allow higher overall sensitivity.

(2) Obligate dim-light foraging

In general bees are most diverse in regions with Mediterranean or xeric climates, and are relatively less diverse in the world's tropics (Michener, 2007). A striking observation on the evolution of dim-light foraging is that it recurs frequently in deserts and tropical forests (Table 1), so its evolution does not track diversity *per se*. Hurd & Linsley (1975), for example, list 90 species of bees that visit *Larrea* in the southwest deserts of the U.S.A.; of these species, 12 (13.3%) visited the host plant almost exclusively under dim-light conditions. One of the largest radiations of dim-light foragers occurs in the genus *Megalopta* (Halictidae), which is exclusively neotropical, except for species that extend north to sub-tropical México and below the Tropic of Capricorn in Brazil and northern Argentina (Moure & Hurd, 1987; Moure, Urban & Melo, 2007; Santos, Melo & Silveira, 2008). This obligate behaviour, however, is not restricted to xeric or tropical regions (Linsley 1958, 1960): *Lasioglossum* (*Sphecodogastra*) (Halictidae), for example, occurs at mid-latitudes in North America, extending into southern Canada (McGinley, 2003; Zayed & Packer, 2007).

Obligate dim-light foraging has evolved at least 19 times, and is known from the Colletidae, Andrenidae, Halictidae and Apidae (Fig 1, Table 1). The extent to which taxa of dim-light bees have diversified varies considerably (see Table 1). A number of taxa are monotypic (e.g. Halictidae - *Rhinethula denticrus* Friese and *Megommation insigne*). Others are relatively speciose, such as the Diphaglossinae, which is a subfamily of mainly crepuscular bees (reviewed in Rozen, 1984). Some parasitic bees, such as *Megalopta* (*Noctoraptor*), have been

reared from dim-light hosts (e.g. Biani & Wcislo, 2007), or have been collected at light traps, and have similar flight times to their hosts (T. Gonzales-Ojeda, S. M. Tierney & W. T. Wcislo unpublished data). The parasite *Odyneropsis apicalis* Ducke was reared from nests of *Ptiloglossa fulvopilosa* Cameron (F. D. Bennett, cited in Rozen, 1966), which may be fully nocturnal (Vesey-Fitzgerald, 1939). Rozen (1984) reports that *O. apicalis* have enlarged ocelli, as do other species of *Odyneropsis* in the collections of the American Museum of Natural History, suggesting they also are dim-light parasites. Other dim-light parasitic species have enlarged ocelli (e.g. *Megalopta*: Engel, Brooks & Yanega, 1997; Biani & Wcislo, 2007). By contrast, parasitic *Triepeolous* that are associated with the maternal *P. arizonensis* Timberlake have normal-sized ocelli and were collected after sunrise (Rozen, 1984).

(a) Phenotypic changes associated with obligate dim-light foraging

(i) *Optics and the visual system.* Natural historians have long recognised that some bee lineages were active under dim-light conditions because of their enlarged simple eyes (ocelli) and their enlarged compound eyes (e.g. Bingham, 1897; Cockerell, 1923; Graenicher, 1911; Rau, 1933). Jander & Jander (2002) showed that the following ocular traits of diurnal bees are invariant when scaled to body size: size and shape of the compound eyes; number of ommatidia per eye; average size of ommatidia; visual acuity (as measured by inter-ommatidial angle); and resolution (as measured by the eye parameter, the product of the inter-ommatidial angle and lens diameter; for criticisms of this parameter, see Horridge, 2005). Set against these allometric patterns, deviations seen in dim-light bees are conspicuous (also see Kelber *et al.*, 2006). Enlarged ocelli and compound eyes are diagnostic for dim-light foraging in bees, but not all dim-light foraging bees have enlarged ocelli and compound eyes.

These optical changes are derived traits that should enable the capture of more photons (e.g. Kerfoot, 1967a; Jander & Jander, 2002; Warrant *et al.*, 2006; Kelber *et al.*, 2006; Warrant, 2008). In one dim-light species, *Megalopta genalis* Meade-Waldo (Halictidae, Augochlorini), derived optical traits increase sensitivity by about 27 times, but by themselves do not provide a sufficient increase in photon capture to sustain visually mediated tasks, such as homing to the nest (Warrant *et al.*, 2004). Additional neurophysiological traits also enhance sensitivity. For example, photoreceptors in *M. genalis* are larger and have a wider angle of acceptance and a slower integration time, both of which further increase the sensitivity of the visual system (Warrant *et al.*, 2004; Greiner, Ribí & Warrant, 2005). At most light levels the photoreceptors of *M. genalis* encode less information than do those of a diurnal *Lasioglossum* (Halictidae, Halictini), but the former possess much greater contrast gain (response per unit contrast), so that information capacity is sacrificed for increased sensitivity (Fredericksen, Wcislo & Warrant, 2008). Neuroanatomical studies of *M. genalis* show that neurons (short visual fibres) descending from photoreceptors have extensive lateral branches, which are unknown in diurnal bees (e.g. Warrant *et al.*, 2004;

Greiner *et al.*, 2005). These neuroanatomical changes are consistent with the hypothesis that photoreceptors share information among adjacent ommatidia (e.g. Warrant *et al.*, 2004; Theobald *et al.*, 2006), which theoretically enhances sensitivity at the cost of reduced acuity (Theobald *et al.*, 2007). Detailed neurobiological studies are needed for other dim-light taxa to assess the generality of these findings, although there is limited corroborating evidence from other Hymenoptera (e.g. Greiner, 2006; Greiner *et al.*, 2007*b*). Nothing is known of the molecular evolution of photoreceptor and visual pigment genes in dim-light bees relative to diurnal taxa (see Yokoyama & Yokoyama, 1996, for a review on vertebrates).

In addition to compound eyes, bees possess three ocelli on the dorsal surface of the head, which are single-lens eyes arrayed in a triangle. Although they likely have different roles in different insects, it is commonly believed that they play a major role in stabilising flight, by detecting and comparing changes in light intensity and thereby controlling pitch, yaw and roll (see Mizunami, 1994). The ocelli of nocturnal bees are larger than those of crepuscular species, which in turn are larger than those of diurnal species (Kerfoot, 1967*a*; McGinley, 2003; Warrant *et al.*, 2006; Somanathan *et al.*, 2008). Relative to diurnal species, the ocelli of *Megalopta* are centered very dorsally, as is also true for a nocturnal wasp, *Apoica* (Warrant *et al.*, 2006). Measurements of the back focal distance show that the ocelli of *Megalopta* are highly under-focused and therefore unable to resolve spatial detail; they also have comparatively very large and tightly packed rhabdoms (light receptors). These two facts suggest that their ocelli are very sensitive to just noticeable differences in ambient light intensity. At present, however, behavioural data are lacking to corroborate these anatomical observations.

(ii) *Body size and colouration.* Crepuscular and nocturnal bees are often thought of as being quite large in body size, relative to related diurnal taxa (Linsley & Cazier, 1970; Hurd & Linsley, 1975; Linsley, 1978; Eickwort & Ginsberg, 1980). *Colletes stephensi*, for example, is a rare colletid bee that is active in dim light, and is one of the larger *Colletes* in America north of Mexico (Hurd & Powell, 1958). Most *Perdita* (Andrenidae) are small to minute bees, but the dim-light *P. (Xerophasma)* is relatively large (Fig. 2). Among the nearly 20,000 species, bee body size (length) varies extensively among diurnal species, from minute (1.8 mm) to very large (39 mm), while bees known to forage under dim light range in length from approximately 8 to 33 mm (Fig. 2).

Using categorical comparisons of body size distributions for the genera of North and Central America ($N = 169$), the proportions of the diurnal and dim-light fauna with “moderate” body sizes are very similar, while there are proportionally fewer dim-light taxa with minute and small body sizes, and proportionally more dim-light taxa with large and very large body sizes, relative to diurnal taxa (Table 2). Using all size categories, a goodness of fit likelihood ratio G -test with William’s correction showed that the deviation in body size of dim-light taxa from the expected distribution derived from diurnal taxa was not significant ($G_{\text{adj } 4} = 8.283$, $P > 0.05$). Expected values for the

minute and very large size categories were low (approximately 5.19 and 0.9, respectively), so following Sokal & Rohlf (1995) we pooled these categories (minute + small, and large + very large) and found a significant deviation in body size distributions of diurnal and dim-light taxa in North and Central America ($G_{\text{adj } 2} = 6.416$, $P < 0.05$).

The fact that many dim-light taxa are relatively large-bodied, and there are no extremely small dim-light species (Fig. 2), may be associated with two physical constraints. First, both intra- and inter-specifically, larger bees tend to have larger compound eyes with larger ommatidia (see Section III. 1*a*). Large body size may be conducive to dim-light activity because of the concomitant increase in photon capture (Jander & Jander, 2002). Secondly, dim-light species are often active at cooler temperatures, especially pre-matinal foragers in deserts, montane regions or higher latitudes (e.g. LaBerge & Thorp, 2005). The facultatively dim-light *Xylocopa (M.) tenuiscapa* (body length: approximately 33 mm), for example, can fly at night in the Western Ghats of India, where night-time temperatures are as low as 2°C, and is larger than the sympatric and nocturnal *X. (Nyctomelitta) tranquebarica* (Somanathan & Borges, 2001; Somanathan *et al.*, 2008). Large bees tend to lose heat more slowly than smaller ones (see e.g. Pereboom & Biesmeijer, 2003), and are better overall at thermoregulation (e.g. Bishop & Armbruster, 1999), which would be advantageous when foraging at cooler temperatures. Some exceptions to these patterns are found in unusual environments. Both workers and drones of the facultatively dim-light honey bee, *A. dorsata*, for example, are significantly smaller than those of their diurnal sister species, the giant honey bee *Apis laboriosa* (Sakagami *et al.*, 1980; McEvoy & Underwood, 1988). In this case, the larger size of *A. laboriosa* is purported to be a response to environmental extremes of the sub-alpine Himalayas where *A. laboriosa* endure temperatures between -5° and 10° C for much of the year (Sakagami *et al.*, 1980; Roubik, Sakagami & Kudo, 1985; Otis, 1996), which approaches the critical limit for bees. *A. laboriosa* are not known to fly under dim-light conditions (Kirchner *et al.*, 1996; Otis, 1996).

Some studies allude to a relationship between time of foraging and body size and colour in diurnal bees, such that larger or darker species are the first to visit flowers in the morning, and as the day proceeds progressively smaller and lighter coloured taxa arrive (e.g. Hurd & Linsley, 1975; Smith & Knapp, 2002). Many dim-light taxa are also relatively pale in body colour, though again exceptions exist. Indeed, a montane species of *Megalopta (M. atra)* Engel is particularly dark-coloured relative to congeneric species (Engel, 2006; Tierney, Gonzales-Ojeda & Wcislo, 2008*a*), and the diurnal sister genus to *Megalopta*, *Xenochlora*, has both light- and dark-coloured species (Engel *et al.*, 1997; Tierney, Gonzales-Ojeda & Wcislo, 2008*b*). All nocturnal *Xylocopa* females are dark, yet so are many diurnal *Xylocopa*. Consequently, pale colouration is not a consistent diagnostic marker for dim-light foraging. Melanisation plays important roles in thermoregulation and protection from ultraviolet light (UV) in insects (see Ellers & Boggs, 2004), but no studies are available to assess whether reduced exposure to UV helps explain colouration trends in dim-light bees.

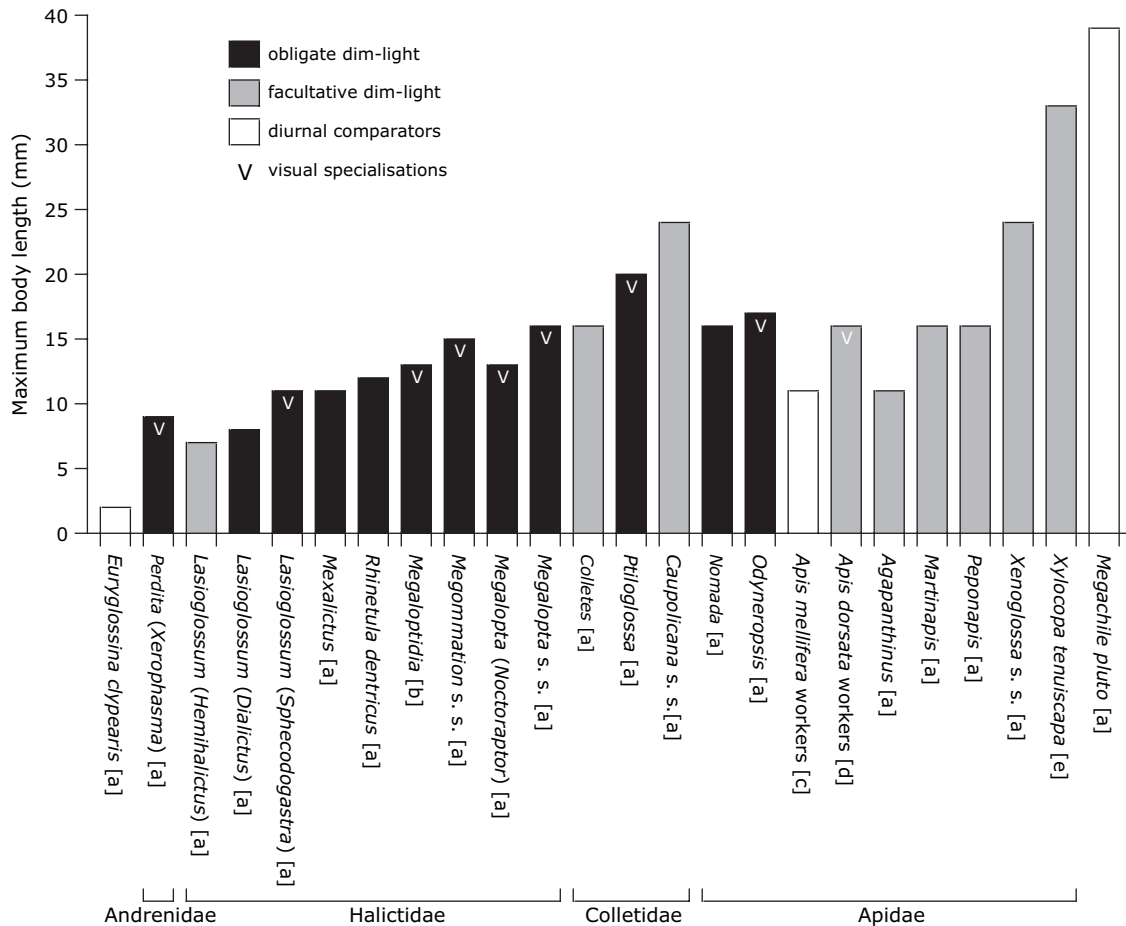


Fig. 2. Range of body size in dim-light bees, giving the maximal body lengths (mm) for taxa for which data are available. For comparisons with diurnal taxa, *Euryglossina* (Colletidae) and *Megachile* (Megachilidae) represent the smallest and largest known bees, respectively, while *Apis mellifera* is included as a size reference because it the most commonly known bee. Taxa with specialised external morphology related to vision in dim-light environments are denoted by “V.” Data sources: a – Michener (2007); b – Engel & Brooks (1998); c – Kajojobe (2007); d – Sakagami *et al.* (1980); e – Somanathan & Borges (2001).

(iii) *Wing morphology.* Aspects of wing morphology of bees scale with body size, such that larger species have decreased relative stigma area; distal extension of wing vein components; increased aspect ratio; and a proximal shift in the centroid of the wing area (Danforth, 1989). The exceptions to these nearly universal scaling rules are dim-light bees and other nocturnal Hymenoptera. *Perdita* (*Xerophasma*) *bequaertiana* Cockerell is one of the largest species of *Perdita*, yet its wing morphology is typical of a small species, having a large stigma, a low aspect ratio and low wing loading (Danforth, 1989). Similar features characterise the wings of other dim-light bees such as *Megalopta* and *Lasioglossum* (*Sphexodogastra*), and other nocturnal Hymenoptera like *Ophion* (Ichneumonidae) and *Macrocentrus* (Braconidae) (Danforth, 1989), even though they tend to be larger bodied than their diurnal relatives. In comparison with related diurnal taxa (Augochlorini), the wings of dim-light *Megalopta* have relatively more hooks (hamuli) that hold the fore- and hind-wings together in flight (Eickwort, 1969), presumably creating a more rigid flight surface. Nothing is known about the aerodynamic flight behaviour of dim-light bees, though the traits described above may

be associated with slower flight speeds needed to avoid collisions in the dark. Slower flight speeds, in turn, might be related to the speed at which photoreceptors process information, but detailed studies are lacking.

(3) Onset of activity in dim-light bees

At least in some bees increasing light levels cue the onset of maternal foraging behaviour (e.g. Lutz, 1931; Kelber *et al.*, 2006), although circadian clocks also entrain rhythmic activity (e.g. Moore, 2001; Fuchikawa & Shimizu, 2007; Yuan *et al.*, 2007). Anecdotal observations suggest that the precocious onset of foraging in *Megalopta* (Kelber *et al.*, 2006; W. T. Wcislo personal observations) and *Xylocopa* (S. M. Tierney personal observations) can be induced by means of artificial illumination. Nothing is presently known about genetic mechanisms associated with circadian rhythms in dim-light bees, but in a vertebrate, the subterranean mole rat (*Spalax ehrenbergi* Nehring), a shift from diurnal to nocturnal activity is associated with an uncoupling of light input as a *zeitgeber* and the circadian clock (Oster *et al.*, 2002).

Table 2. Categorical body size distributions of North and Central American bee genera (from Michener *et al.*, 1994). Data are tabulated giving overall size distributions, and again according to the light environments in which they forage

	Body size categories					Total
	Minute	Small	Moderate	Large	Very large	
Frequency of genera	23	79	95	53	7	257
% of 169 genera	13.61%	46.75%	56.21%	31.40%	4.14%	
Light conditions						
Dim-light						
Obligate	2	4	5	3	0	14
Facultative	0	8	15	11	3	37
Pooled:	2	12	20	14	3	51
Diurnal	21	67	75	39	4	206
<i>G</i> -test expected value:	5.2	16.59	18.57	9.65	0.99	51
Proportion by size						
Dim-light						
Obligate	14.29%	28.57%	35.71%	21.43%	0.00%	
Facultative	0.00%	21.62%	40.54%	29.73%	8.11%	
Pooled:	3.92%	23.53%	39.22%	27.45%	5.88%	
Diurnal	10.19%	32.52%	36.41%	18.93%	1.94%	

(4) Homing and orientation behaviour and nocturnal flight

Based on studies of *M. genalis* and *Xylocopa tranquebarica*, females use visual cues such as local landmarks to orient to their nest (Warrant *et al.*, 2004; Somanathan *et al.*, 2008), as do diurnal bees (e.g. see references in Wcislo, 1992). Nothing is known about long-distance orientation, though the ommatidia along the dorsal rim of the compound eye of *M. genalis* are highly sensitive to polarized light (Greiner *et al.*, 2007a), and are typical of hymenopterans that use polarized light for long-distance orientation. Light is strongly polarized in the tropics, including at dawn and dusk (Shashar *et al.*, 1998; Cronin, Warrant & Greiner, 2006). Comparative studies are lacking for most other dim-light bees.

IV. CORRELATED EVOLUTION IN DIM-LIGHT BEES

Using Engel's (2000) phylogeny for the tribe Augochlorini (Halictidae) there is a strong association between characters associated with dim-light foraging such that changes in the size of ocelli and foraging times (relative to light levels) are concentrated at certain nodes of the tree ($P < 0.001$). This result is stable under different random resolutions of polytomies. Given observations of facultative dim-light foraging in taxa without enlarged ocelli or compound eyes, this pattern suggests that the behavioural trait (i.e. foraging time) drives the subsequent evolution of anatomical traits. There is no evidence that any of the external morphological traits for dim-light foraging occur in sister taxa with diurnal foraging behaviour within Halictidae.

Information on bee taxa with obligate dim-light foraging (Table 1) is consistent with results from a concentrated changes test for the Augochlorini. For 11 comparisons at

least some members of a taxon with obligate dim-light foraging show anatomical features that underlie the novel behaviour. The other comparisons either show no conspicuous anatomical features or they have not been reported; these latter cases all involve taxa that fly at or near sunrise and sunset, at moderately bright light levels. Derived anatomical features that are associated with dim-light foraging (e.g. enlarged compound eyes or ocelli) do not occur in diurnal species. Likewise, there are no cases of obligate dim-light foraging in lineages that do not also contain facultative dim-light foraging.

Within lineages degree of anatomical change is associated with the dimness of the environment. The speciose sweat bee genus *Lasioglossum* (Halictini), for example, contains numerous subgenera (e.g. McGinley, 1986; Michener, 2007; Danforth, Conway & Ji, 2003a), and nearly all *Lasioglossum* s.l. have diurnal foraging. The subgenus *L. (Sphecodogastra)*, however, comprises eight species, all of which are crepuscular or nocturnal (Chandler, 1961; Kerfoot, 1967b,c; McGinley, 2003). Bee taxonomists have long used the ratio of the lateral ocellus diameter (simple eye) to the distance between the ocellus and the compound eye, to describe ocellar size relative to head shape. For crepuscular species of *L. (Sphecodogastra)* this ratio ranges from 1.18 to 2.0, while in two species (probable sister species) that are thought to have nocturnal activity the ratio ranges from 0.33 to 0.35 (McGinley, 2003). The diurnal sister taxon to *L. (Sphecodogastra)* is *L. (Evyllaesus)* (Danforth *et al.* 2003a), and in the latter this ratio ranges from 1.9 to 2.25. We lack a phylogenetic hypothesis for *L. (Sphecodogastra)* species and do not know if there was progressive evolution towards increasingly large ocelli, but it is clear that species that are active under the dimmest conditions have the largest ocelli. Similar variation in ocelli size with respect to light environments is known for some carpenter bees (*Xylocopa*) (Minckley, 1998; Somanathan *et al.*, 2008).

V. THE ECOLOGY OF DIM-LIGHT FORAGING: ESCAPE FROM ENEMIES AND COMPETITORS?

The evolution of dim-light foraging in bees may be driven by ecological advantages associated with an escape from competitors and natural enemies (e.g. Wcislo *et al.*, 2004), although much of the supporting evidence is circumstantial.

(1) Pollen competition and resource utilisation

Bees that forage at night are presumed to face reduced competition for resources (e.g. Wcislo *et al.*, 2004; Kato, 2006). The role of competition in explaining resource specialization in bees has been inferred mainly from visitation rates (e.g. Minckley *et al.*, 1994; Minckley, Cane & Kervin, 2000; reviewed in Wcislo & Cane, 1996), but no studies have linked differential visitation rates to pollen harvesting and rates of cell provisioning. A Mexican species of *Megalopta*, for example, visits *Ipomoea wolcottiana* Rose before sunrise, after which 20 diurnal species visited to collect pollen (Bullock *et al.*, 1987). The crepuscular desert bee *Xylocopa (Proxycopa) olivieri* Lepeletier shows a small peak of foraging activity in the morning before sunrise when no other bees are flying except for very small numbers of honeybees (*Apis mellifera* L.). *X. (P.) olivieri* are mostly inactive during the day when other bees are foraging, and have a larger peak of activity in the evening after sunset when there are no other bees active (Gottlieb *et al.*, 2005; for other examples, see Roulston, 1997; Bullock *et al.*, 1987).

Unlike many diurnal bees (e.g. Minckley *et al.*, 1994), obligate dim-light bees do not always track resource availability. Species of *Megalopta* in central Panama cease foraging at a time in the evening (near astronomical twilight), even though pollen is still abundant (W.T. Wcislo personal observations), presumably because of visual constraints (see Section III. 2*ai*). By contrast, according to Somanathan & Borges (2001), the facultative dim-light bee, *X. tenuiscapa*, tracks resource availability to some extent. It was the major nocturnal visitor to flowers of the night-blooming tree, *Heterophragma quadriloculare* (Bignoniaceae), and bee visitation was significantly highest at peak anthesis near sunset, although smaller numbers of bees were recorded at other times throughout the night, well after astronomical twilight. A subsequent study from the same site presented contradictory observations that the flight activity of *X. tenuiscapa* was largely diurnal, with occasional extensions of foraging activity into crepuscular periods (prior to astronomical twilight) (Somanathan *et al.*, 2008). The giant honey bee (*Apis dorsata*) is another facultative dim-light forager that extends its foraging activity when night-blooming flowers are available, but the extent to which it tracks diel resource availability of the night-blooming flora is not known (Momose *et al.*, 1998).

Roulston (1997) noted that many of the flowers used by *Megalopta* as pollen sources are frequently associated with bats, which often have pollen with relatively high protein content. He hypothesised that access to particularly rich pollen sources may favour the evolution of nocturnal behaviour. A more recent study, however, casts doubt on

this hypothesis because the protein content of pollen from bat-pollinated or other zoophilous flowers is not different, on average, from that of anemophilous plants, once phylogeny is taken into account (Roulston, Cane & Buchmann, 2000). A related idea is that many tropical trees associated with bats have relatively long flowering phenologies (Wright & Calderón, 1995; Borchert, 1983), and each flower typically has large quantities of pollen, so quantity and predictability of resources may be more important than quality (e.g. Somanathan & Borges, 2001).

A conventional assumption is that the evolution of bats and bat-pollinated trees (Park, 1940; Baker & Harris, 1957; Baker, 1961; Marshall, 1983; Hopkins, 1984; Eguiarte & Burquez, 1987; Gribel & Hay, 1993) opened a niche for bees to exploit. This hypothesis is likely to be true in some cases, but in other cases phylogenetic evidence casts doubt on it. The pantropical tree genus *Parkia* (Leguminosae) contains a clade of species with flowers that are characteristic of bat pollination, while another clade has entomophilous flowers (Hopkins, 1984; Luckow & Hopkins, 1995). A phylogenetic study of *Parkia* indicates that the bat-pollinated clade is derived relative to the insect-pollinated clade (Luckow & Hopkins, 1995). Hopkins, Hopkins & Sothers (2000) report that the primary visitors to flowers of a Brazilian species of *Parkia* are *Megalopta* sp., and they suggest that pollination by a nocturnal bee such as *Megalopta* may facilitate a shift to bat pollination. By contrast, a species of *Parkia* (*P. clappertoniana* Keay) in Ghana is pollinated by bats, and although bees (*Apis mellifera*) collect its pollen at dusk and dawn, it is thought they play no role in pollination because they confined their visits only to the staminate parts of the inflorescences (Baker & Harris, 1957).

(2) Escape from natural enemies

Rydell & Speakman (1995) suggested that the evolution of nocturnal behaviour in bats might be associated with advantages that accrue from moving into enemy-free space, at least early in their evolution (see also Beauchamp, 2007, for other vertebrates). A similar suggestion has been made for dim-light bees (e.g. Wcislo *et al.*, 2004). For bees, scant evidence for this hypothesis is equivocal. Various insects attack nests and brood of *Megalopta*, including ants, flies, beetles, wasps and parasitic *Megalopta* (e.g. Biani & Wcislo, 2007; Cambra, Gonzalez & Wcislo, 2005; Smith, Wcislo & O'Donnell, 2003; Falin, Arneson & Wcislo, 2000; Smith, Wcislo & O'Donnell, 2008), as does an unidentified predator, presumably an anteater-like vertebrate (W. T. Wcislo personal observations). Survivorship curves for colonies of dim-light *Megalopta* are not different in shape from those of several diurnal halictine bees, and 50% survivorship rates are slightly better or roughly comparable (Smith *et al.*, 2003; Wcislo *et al.*, 2004; Bata, 1966; Michener & Wille, 1961; Sakagami & Fukuda, 1989), suggesting that there is at best a modest escape from enemies. Rates of cell parasitism, however, are approximately 5-6% for *Megalopta* (Wcislo *et al.*, 2004), while mean rates of cell parasitism for diurnal bees range from 24 to 29% (Wcislo, 1996). Lower cell parasitism rates could be

interpreted as an escape from enemies by nocturnal species. Alternatively, the narrow foraging window (approximately 1 h post-sunset and 1 h pre-sunrise) of *Megalopta* in Panamá (Warrant *et al.*, 2004; Wcislo *et al.*, 2004; Kelber *et al.*, 2006), relative to diurnal species, means that even solitary nests will be un-occupied less frequently than in diurnal species, and more frequently will have a *de facto* guard.

VI. DISCUSSION

Among bees a recurrent facultative phenotype involves opportunistic dim-light foraging (see Fig. 1). Such behaviour is presumably advantageous in that it enables access to floral resources when most competitors are not foraging (e.g. Roubik, 1989; Wcislo *et al.*, 2004; Somanathan, Borges & Chakravarthy, 2004; Gottlieb *et al.*, 2005; Somanathan *et al.*, 2006). In desert regions these activity patterns may also minimise exposure to unfavourable thermal conditions (e.g. Willmer & Stone, 1997; Gottlieb *et al.*, 2005). Likewise, tropical diurnal species sometimes fly at high ambient temperatures, and run the risk of overheating as they reach thoracic temperatures near lethal limits (see Pereboom & Biesmeijer, 2003). Presumably such advantages would accrue to individuals that facultatively exploit dim-light environments, although relevant data are scarce.

Beauchamp (2007) reviewed studies of predation in birds and mammals, and showed that qualitative levels of predation were higher during the day than at night for 78% and 73% of the populations of the two taxa, respectively. Detailed quantitative studies are generally lacking, however, but in general these results are consistent with the hypothesis that the evolution of nocturnalism is associated with reduced predation risk. Mougeot & Bretagnolle (2000) showed that predation risk in nocturnal seabirds was higher on moonlit nights than dark nights, suggesting that darkness provides cover against visually guided predators. As reviewed above, data on cell parasitism rates for bees are consistent with this hypothesis, but overall rates of nest survival are sometimes inconsistent with it.

For insects with apposition eyes a shift into a dim-light environment creates a substantial problem in sensory ecology (see Section III. 2). Due to a trade-off between sensitivity and acuity in the design of compound eyes, diurnal species typically have high-resolution eyes with low sensitivity (Jander & Jander, 2002), and thus performance is reduced under low-light conditions (see Theobald *et al.*, 2007). Consequently, at least some dim-light bees evolved a suite of optical traits that increase the numbers of photons captured, providing a better signal to noise ratio in dim light, and neural changes increase sensitivity as well (for examples in ants, see Menzi, 1987; Greiner *et al.*, 2007b). Functionally equivalent optical changes have been demonstrated for other dim-light insects and vertebrates, including wasps (*Apoica*) (Greiner, 2006), alates of leaf-cutting ants (*Atta*) (Moser *et al.*, 2004), army ants (Coody & Watkins, 1986), mosquitoes (Land *et al.*, 1999; Kawada *et al.*, 2006), butterflies (Yack *et al.*, 2007), birds (Garamszegi, Möller & Erritzoe, 2002; Thomas *et al.*, 2006; Hall & Ross, 2007) and

primates (Ross & Kirk, 2007). Vision in dim-light conditions is clearly enhanced by having larger eyes, but increases in eye size are associated with significant energetic costs. A law of diminishing returns applies to sensory systems because excess functional capacity is strongly penalised due to increased energetic costs associated with information processing (see Niven & Laughlin, 2008). Consequently, dim-light bees face strong selective pressures to evolve eye sizes that just meet functional demands but do not exceed them (see Fredriksen & Warrant, 2008, for an example from butterflies).

Light sensitivity varies among dim-light bee taxa, as inferred from behavioural evidence (Table 1). Some dim-light bees are sensitive to lunar phases and prolong their foraging activity when the moon is bright (e.g. Kerfoot, 1967a), while others do not (e.g. Kelber *et al.*, 2006; Somanathan *et al.*, 2008). We lack comparative data to assess whether these behavioral differences are associated with differences in neural design that limit photon capture (e.g. Warrant *et al.*, 2004; for an example in birds, see Martin *et al.*, 2004). In addition, some of the behavioural differences may be due to environmental factors. Obligate dim-light bees that are sensitive to lunar periodicity (Kerfoot, 1967a) forage in relatively open areas, while those that are apparently insensitive (e.g. *Megalopta genalis*) nest in the understorey of a tropical forest where moonlight is blocked by the canopy. Other *Megalopta* that live in forests with a more open canopy (e.g. tropical dry forests of Jalisco and Nayarit, Mexico) continue to fly into the night (R. Ayala, personal communication). Similar variation is known within species. In India, for example, *X. tranquebarica* continues to fly at night after astronomical twilight (Somanathan *et al.*, 2008), while the same species in Thailand flies on moonlit nights but not moonless ones (Burgett & Sukumalanand, 2000). Comparative neurobiological and ecological data are not available to assess whether inter- and intra-specific differences in foraging patterns are due to differences in the visual systems of bees in different populations and species, or to differences in forest canopy architecture and resulting light environments. Experimental manipulations indicate that decreased light levels retard onset of activity in *Megalopta*, indicating that bees can respond to local variation in light levels (T. Gonzales-Ojeda, S. M. Tierney & W. T. Wcislo, unpublished data).

Dim-light foraging appears to be especially common in two life zones: tropical forests and desert regions. What factors may help to explain why dim-light foraging has apparently gone to fixation (obligate dim-light species) more often in the tropics, as is true for other taxa such as paper wasps (Vespidae) (Hunt, Jeanne & Keeping, 1995), as well as in xeric temperate regions? Important sources of pollen for neotropical *Megalopta* are plants (e.g. *Ceiba*, *Pseudobombax*) that are typically associated with vegetarian bats, although a number of other plants are used as well (Wcislo *et al.*, 2004; A. Smith & W.T. Wcislo, unpublished data). Baker (1961) and Stebbins (1970) discuss features of tree and floral architecture that are required for bat pollination (e.g. large nectar-producing flowers set on sturdy branches; free-flying space around the flowers; flower availability over an extended time period), and they note that species with such

traits are restricted to tropical and sub-tropical regions. Night-blooming plants represent a greater percentage of the local flora in the tropics relative to the temperate zone (Endress, 1994). Thus, resource availability *per se* may help explain this biogeographic pattern, but would not account for why traits go to fixation.

Close to the equator (e.g. Panama, $\sim 9^{\circ}$ N latitude) sunrise and sunset are associated with sharp changes in light intensity that span almost four orders of magnitude over approximately one hour, and at the steepest part of the slope light levels change by a factor of 10 in approximately 10 min (Theobald *et al.*, 2007). By contrast, twilight is considerably longer at higher latitudes during the summer. Slight differences in timing of activity should have greater consequences in the tropics relative to the temperate zone therefore, because of more intense selection in the former. Differences in timing of foraging activity, relative to unfavourable environmental conditions, also may help explain the recurrence of obligate dim-light foraging in xeric areas, where the bee fauna is particularly diverse (Michener, 2007) and many species are pollen specialists (oligolectic) (e.g. Linsley, 1958; Hurd & Linsley, 1964, 1975; Wcislo & Cane, 1996; Minckley *et al.*, 2000). Local populations of oligolectic bees show high degrees of genetic differentiation (e.g. Danforth, Ji & Ballard, 2003*b*), including the dim-light species, *Lasioglossum (Sphecodogastra) oenotherae* (Zayed & Packer, 2007). Population genetic structure presumably arises because local populations track local variation in flowering phenology (e.g. Danforth, 1999), which in turn is related to local variation in rainfall (e.g. Minckley *et al.*, 2000). Plant taxa that are pollen sources for many dim-light xeric species (e.g. Onagraceae and Curcubitaceae; Linsley, MacSwain & Raven, 1963, 1964; Hurd & Linsley, 1964) show divergent reproductive traits associated with local variation in aridity (e.g. Evans *et al.*, 2005). Stebbins (1970) discussed how the environment can be a limiting factor for angiosperm reproduction because of its influence on how much time is available for flower development under the particular conditions at the time of pollination. He illustrated this point by discussing how floral adaptations to moth pollination, including changes from diurnal to matinal, vespertine or nocturnal flowering, are expected to occur more often in hot dry climates, where day-time conditions are unfavourable for flowering and pollination. Thus, the repeated evolution of dim-light foraging in xeric areas may be related to bees tracking shifting flowering phenologies. These considerations also raise the question of what factors facultatively induce individuals to invade an extreme environment?

In the temperate zone, inter-annual variation in rainfall and other abiotic factors is associated with variation in resource availability for bees (e.g. Minckley *et al.*, 1994; Minckley *et al.*, 2000). A popular misconception holds that such abiotic factors are relatively unimportant, or at least they are more stable in the tropics. In an influential paper, Dobzhansky (1950, p. 220) wrote that in the tropics “physical conditions are easy.” In fact, inter-annual variation in abiotic conditions, particularly the El Niño Southern Oscillation (ENSO), recurrently leads to severe stress in many parts of the humid tropics (e.g. Wright, 2005).

ENSO events have important consequences for plant reproduction due to changes in rainfall, temperature and irradiance (Wright and Calderón, 2006). Mild El Niño events tend to increase flowering, which should be advantageous for bees, but severe events will decrease plant reproduction. Although such events should cause famine among animals that depend on floral resources for food, as it does for mammals that depend on fruits (Wright *et al.*, 1999), evidence for bees is mixed (see e.g. Roubik, 2001; Frankie *et al.*, 2005 and references therein).

Rau (1933) postulated that innovation, with respect to feeding, was especially likely in times of stress, which may force individuals to switch to novel resources in an opportunistic way, facilitated by learned associations (see also Wcislo, 1989; West-Eberhard, 2003). Specialist bees, *Andrena (Diandrena) Cockerell*, for example, usually collect pollen only from one or a few plant species, but use alternative resources when their preferred pollen sources are absent or rare due to environmental stresses (Thorp 1979). Bees are well known for their abilities to learn when food is available (e.g. Frisch, 1967; Boisvert, Veal & Sherry, 2007) and track it subsequently (Momose *et al.*, 1998). If stress conditions force individuals to forage outside their normal window of foraging times, then learning could stabilise the novel foraging activity, and set up conditions that modify selective pressures and promote phenotypic innovation, as discussed by Mayr (1960) and others (e.g. Wcislo, 1989; West-Eberhard, 2003, pp. 337ff.; Beltman, Haccou & ten Cate, 2004).

VII. CONCLUSIONS

(1) Temporal patterns of the foraging behaviour of bees vary extensively; individuals of most species are diurnal foragers and fly under bright sun, although facultatively dim-light foraging has evolved repeatedly in most major lineages.

(2) Obligate dim-light foraging has a more restricted phyletic distribution, yet has evolved independently a minimum of 19 times. Some dim-light taxa restrict their foraging behaviour to early morning (matinal), others to early evening (vespertine) or both (crepuscular), while some species are fully nocturnal (i.e. foraging after astronomical twilight).

(3) Facultative dim-light foragers show no external structural traits in their visual systems (with one exception) that enable visually mediated flight behaviours in low-light environments, while most obligate dim-light foragers show a suite of convergent optical traits, including enlarged simple eyes (ocelli) and compound eyes, as well as larger ommatidia in the compound eyes.

(4) Intensive neurobiological studies of *Megalopta genalis* (Halictidae) show that a dim-light species has also evolved a series of neurological traits that enhance photon capture, including larger photoreceptors with slower integration times and greater contrast gains. The generality of these neurobiological observations remains to be determined.

(5) Escape from competition for pollen and nectar resources, and escape from natural enemies, are hypothesised to be driving factors in the evolution of obligate dim-light foraging, but few data are available to test these hypotheses.

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IX. REFERENCES

- BAKER, H. G. (1961). The adaptation of flowering plants to nocturnal and crepuscular pollinators. *The Quarterly Review of Biology* **36**, 64–73.
- BAKER, H. G. & HARRIS, B. J. (1957). The pollination of *Parkia* by bats and its attendant evolutionary problems. *Evolution* **11**, 449–460.
- BALDWIN, J. M. (1902). *Development and Evolution*. MacMillan, New York.
- BARTHELL, J. F. & KNOPS, J. M. H. (1997). Visitation of evening primrose by carpenter bees: evidence of a “mixed” pollination syndrome. *The Southwestern Naturalist* **42**, 86–93.
- BATRA, S. W. T. (1966). The life cycle and behavior of the primitively social bee, *Lasioglossum zephyrum* (Halictidae). *University of Kansas Science Bulletin* **46**, 359–423.
- BEAUCHAMP, G. (2007). Exploring the role of vision in social foraging: what happens to group size, vigilance, spacing, aggression and habitat use in birds and mammals that forage at night? *Biological Reviews* **82**, 511–525.
- BELTMAN, J. B., HACCOU, P. & TEN CATE, C. (2004). Learning and colonization of new niches: a first step towards speciation. *Evolution* **58**, 35–46.
- BIANI, N. B. & WCISLO, W. T. (2007). Notes on the reproductive morphology of the parasitic bee *Megalopta byroni* (Hymenoptera: Halictidae), and a tentative new host record. *Journal of the Kansas Entomological Society* **80**, 392–394.
- BINGHAM, C. T. (1897). *Fauna of British India, including Ceylon and Burma Hymenoptera. 1. Wasps and bees*. Taylor & Francis, London.
- BISHOP, J. A. & ARMBRUSTER, W. S. (1999). Thermoregulatory abilities of Alaskan bees: effects of size, phylogeny and ecology. *Functional Ecology* **13**, 711–724.
- BOHART, G. E. & YOUSSEF, N. N. (1976). The biology and behavior of *Ezylaeus galpinsiae* Cockrell (Hymenoptera: Halictidae). *The Wasmann Journal of Biology* **34**, 185–234.
- BOISVERT, M. J., VEAL, A. J. & SHERRY, D. F. (2007). Floral reward production is timed by a insect pollinator. *Proceedings of the Royal Society B* **274**, 1831–1837.
- BORCHERT, R. (1983). Phenology and control of flowering in tropical trees. *Biotropica* **15**, 81–89.
- BULLOCK, S. H., AYALA, R., BAKER, I. & BAKER, H. G. (1987). Reproductive biology of the tree *Ipomoea wolcottiana* (Convolvulaceae). *Madroño* **34**, 304–314.
- BURGETT, D. M. & SUKUMALANAND, P. (2000). Flight activity of *Xylocopa (Nyctomelitta) tranquebarica*: a night flying carpenter bee (Hymenoptera: Apoidea). *Journal of Apicultural Research* **39**, 75–83.
- CAMBRA, R. A. T., GONZALEZ, V. H. & WCISLO, W. T. (2005). Description of the male, host associations, and new distribution records for *Lophostigma Mickel* (Hymenoptera: Mutillidae). *Proceeding of the Entomological Society of Washington* **107**, 229–234.
- CHANDLER, L. (1961). Light trap collections of the nocturnal bee, *Sphécodogastra texana* (Cresson) (Hymenoptera, Halictidae). *Proceedings of the Indiana Academy of Science* **71**, 124–129.
- COCKERELL, T. D. A. (1900). Descriptions of new bees collected by Mr. H. H. Smith in Brazil. *Proceedings of the Academy of Natural Sciences of Philadelphia* **52**, 356–377.
- COCKERELL, T. D. A. (1923). Two nocturnal bees and a minute *Perdita*. *American Museum Novitates* **66**, 1–4.
- COCKERELL, T. D. A. & PORTER, W. (1899). Contributions from the New Mexico Biological Station - observations on bees, with description of new genera and species. *Annals and Magazine of Natural History* **4**, 403–421.
- COODY, C. J. & WATKINS, J. F. (1986). The correlation of eye size with circadian flight periodicity of nearctic army ant males of the genus *Neivamyrmex* (Hymenoptera; Formicidae, Ecitoninae). *Texas Journal of Science* **38**, 3–7.
- CRONIN T. W., WARRANT E. J. & GREINER B. (2006). Celestial polarization patterns during twilight. *Applied Optics* **45**, 5582–5589.
- DALY, H. V. (1961). Biological observations on *Hemihalictus lustrans* with a description of the larva (Hymenoptera: Halictidae). *Journal of the Kansas Entomological Society* **34**, 134–141.
- DANFORTH, B. N. (1989). The evolution of hymenopteran wings: the importance of size. *Journal of the Zoological Society (London)* **218**, 247–276.
- DANFORTH, B. N. (1991). Female foraging and intranest behavior of a communal bee, *Perdita portalis* (Hymenoptera: Andrenidae). *Annals of the Entomological Society of America* **84**, 537–548.
- DANFORTH, B. N. (1999). Emergence dynamics and bet hedging in a desert bee, *Perdita portalis*. *Proceedings of the Royal Society, Biological Sciences* **266**, 1985–1994.
- DANFORTH, B. N., CONWAY, L. & JI, S. (2003a). Phylogeny of eusocial *Lasioglossum* reveals multiple losses of eusociality within a primitively eusocial clade of bees (Hymenoptera: Halictidae). *Systematic Biology* **52**, 23–36.
- DANFORTH, B. N., JI S., & BALLARD L. J. (2003b). Gene flow and population structure in an oligolectic desert bee, *Macrotera (Macroteropsis) portalis* (Hymenoptera: Andrenidae). *Journal of the Kansas Entomological Society* **76**, 221–235.
- DARWIN, C. (1872). *The Expression of the Emotions in Man and Animals* (1965 re-print). University of Chicago Press, Chicago.
- DOBZHANSKY, T. (1950). Evolution in the tropics. *American Scientist* **38**, 209–221.
- DUBITZKY, A. (2005). *Studies in phylogeny and biosystematics of bees: The bee genus Andrena (Andrenidae) and the tribe Anthophorini (Apidae) (Insecta: Hymenoptera: Apoidea)*. PhD thesis, Ludwig-Maximilian University, Munich. [<http://edoc.ub.uni-muenchen.de/5452/>]
- DUCKE, A. (1902). Ein neues subgenus von *Halictus* Latr. *Zeitschrift für Systematische Hymenopterologie und Dipterologie* **2**, 102–103.
- DYER, F. (1985). Nocturnal orientation by the Asian honey bee, *Apis dorsata*. *Animal Behavior* **33**, 769–774.

- EGUIARTE, L. & BURQUEZ, A. (1987). Reproductive ecology of *Manfreda brachystachya*, an iteroparous species of Agavaceae. *The Southwestern Naturalist* **32**, 169–178.
- EICKWORT, G. C. (1969). A comparative morphological study and generic revision of the augochlorine bees. *The University of Kansas Science Bulletin* **48**, 325–524.
- EICKWORT, G. C. & GINSBERG, H. S. (1980). Foraging and mating behavior in Apoidea. *Annual Review of Entomology* **25**, 421–446.
- ELLERS, J. & BOGGS, C. L. (2004). Functional ecological implications of intraspecific differences in wing melanization in *Colias* butterflies. *Biological Journal of the Linnean Society* **82**, 79–87.
- ENDRESS, P. K. (1994). *Diversity and Evolutionary Biology of Tropical Flowers*. Cambridge University Press, Cambridge.
- ENGEL, M. (2000). Classification of the bee tribe Augochlorini (Hymenoptera: Halictidae). *Bulletin of the American Museum of Natural History* **250**, 1–90.
- ENGEL, M. (2006). A new nocturnal bee of the genus *Megalopta*, with notes on other Central American species. *Mitteilungen des Internationalen Entomologischen Vereins* **31**, 37–49.
- ENGEL, M. S. & BROOKS, R. W. (1998). The nocturnal bee genus *Megaloptidia* (Hymenoptera: Halictidae). *Journal of Hymenoptera Research* **7**, 1–14.
- ENGEL, M. S., BROOKS, R. W. & YANEGA, D. (1997). New genera and subgenera of augochlorine bees (Hymenoptera: Halictidae). *Science Papers, Natural History Museum, University of Kansas* **5**, 1–21.
- ESTES, J. R. & THORP, R. W. (1975). Pollination ecology of *Pyrrhopappus carolinianus* (Compositae). *American Journal of Botany* **62**, 148–159.
- EVANS, H. E. (1966). *The Comparative Ethology of the Sand Wasps*. Harvard University Press, Cambridge.
- EVANS, M. E. K., HEARN, D. J., HAHN, W. J., SPANGLE, J. M., & VENABLE, D. L. (2005). Climate and life-history evolution in evening primroses (*Oenothera*): a phylogenetic comparative analysis. *Evolution* **59**, 2005, pp. 1914–1927
- FALIN, Z. H., ARNESON, L. C. & WCISLO, W. T. (2000). Night-flying sweat bees *Megalopta genalis* and *Me. ecuadoria* (Hymenoptera: Halictidae) as hosts of the parasitoid beetle *Macrosiagon gracilis* (Cleopectera: Rhipiphoridae). *Journal of the Kansas Entomological Society* **73**, 183–185.
- FRANKIE, G. W., RIZZARDI, M., VINSON, S. B., GRISWOLD, T. L. & RONCHI, P. (2005). Changing bee composition and frequency on a flowering legume, *Andira inermis* (Wright) Kunth ex DC. during El Niño and La Niña years (1997–1999) in northwestern Costa Rica. *Journal of the Kansas Entomological Society* **78**, 100–117.
- FREDERICKSEN, R. & WARRANT, E. J. (2008). Visual sensitivity in the crepuscular owl butterfly *Colias memnon* and the diurnal blue morpho *Morpho peleides*: a clue to explain the evolution of nocturnal apposition eyes? *Journal of Experimental Biology* **211**, 844–851.
- FREDERICKSEN, R., WCISLO, W. T. & WARRANT, E. J. (2008). Visual reliability and information rate in the retina of a nocturnal bee. *Current Biology* **18**, 349–353.
- FRISCH, K. von (1967). *The Dance Language and Orientation of Bees*. Harvard University Press, Cambridge.
- FUCHIKAWA, T. & SHIMIZU, I. (2007). Circadian rhythm of locomotor activity in the Japanese honeybee, *Apis cerana japonica*. *Physiological Entomology* **32**, 73–80.
- GARAMSZEGI, L. Z., MÖLLER, A. P. & ERRITZOE, J. (2002). Coevolving avian eye size in relation to prey capture and nocturnality. *Proceeding of the Royal Society of London B* **269**, 961–967.
- GERLING, D., HURD JR., P. D. & HEFETZ, A. (1983). Comparative behavioral biology of two middle east species of carpenter bees (*Xylocopa* Latreille) (Hymenoptera: Apoidea). *Smithsonian Contributions to Zoology* **369**, 1–33.
- GOTTLIEB, D., KEASAR, T., SHMIDA, A. & MOTRO, U. (2005). Possible foraging benefits of biomodal daily activity in *Proxyclopa olivieri* (Lepelletier) (Hymenoptera: Anthophoridae). *Environmental Entomology* **34**, 417–424.
- GRAENICHER, S. (1911). Bees of northwestern Wisconsin. *Bulletin, Public Museum, Milwaukee City of Milwaukee* **1**, 221–249.
- GRAENICHER, S. (1930). Bee-fauna and vegetation of the Miami region of Florida. *Annals of the Entomological Society of America* **23**, 153–174.
- GREINER, B. (2006). Adaptations for nocturnal vision in insect apposition eyes. *International Review of Cytology* **250**, 1–45.
- GREINER, B., CRONIN, T. W., RIBI, W. A., WCISLO, W. T. & WARRANT, E. J. (2007a). Anatomical and physiological evidence for polarization vision in the nocturnal bee *Megalopta genalis*. *Journal of Comparative Physiology A* **193**, 591–600.
- GREINER, B., NARENDRA, A., REID, S. F., DACKER, M., RIBI, W. A. & ZEIL, J. (2007b). Eye structure correlates with distinct foraging-timing in primitive ants. *Current Biology* **17**, R879–880.
- GREINER, B., RIBI, W. A. & WARRANT, E. J. (2005). A neural network to improve dim-light vision? Dendritic fields of first-order interneurons in the nocturnal bee *Megalopta genalis*. *Cell Tissue Research* **322**, 313–320.
- GRIBEL, R. & HAY, J. D. (1993). Pollination ecology of *Caryocara brasiliense* (Caryocaraceae) in Central Brazil cerrado vegetation. *Journal of Tropical Ecology* **9**, 199–211.
- HALL, M. I. & ROSS, C. F. (2007). Eye shape and activity pattern in birds. *Journal of Zoology* **271**, 437–444.
- HOPKINS, H. C. (1984). Floral biology and pollination ecology of the neotropical species of *Parkia*. *Journal of Ecology* **72**, 1–23.
- HOPKINS, M. J. G., HOPKINS, H. C. F. & SOTHERS, C. A. (2000). Nocturnal pollination of *Parkia velutina* by *Megalopta* bees in Amazonia and its possible significance in the evolution of chiropterophily. *Journal of Tropical Ecology* **16**, 733–746.
- HORRIDGE, A. (2005). The spatial resolutions of the apposition compound eye and its neuro-sensory feature detectors: observation versus theory. *Journal of Insect Physiology* **51**, 243–266.
- HUNT, J. H., JEANNE, R. L. & KEEPING, M. G. (1995). Observations on *Apoica pallens*, a nocturnal Neotropical social wasp (Hymenoptera: Vespidae, Polistinae, Epiponini). *Insectes Sociaux* **42**, 223–236.
- HURD JR., P. D. (1958). Observations on the nesting habits of some new world carpenter bees with remarks on their importance in the problem of species formation (Hymenoptera: Apoidea). *Annals of the Entomological Society of America* **51**, 365–375.
- HURD JR., P. D. & LINSLEY, E. G. (1964). The squash and gourd bees – genera *Peponapis* Robertson and *Xenoglossa* Smith – inhabiting America North of Mexico (Hymenoptera: Apoidea). *Hilgardia* **35**, 375–477.
- HURD JR., P. D. & LINSLEY, E. G. (1967). The squash and gourd bees of the genus *Xenoglossa*. *Annals of the Entomological Society of America* **60**, 988–1007.
- HURD JR., P. D. & LINSLEY, E. G. (1970). A classification of the squash and gourd bees *Peponapis* and *Xenoglossa* (Hymenoptera: Apoidea). In *University of California Publications in Entomology*, vol. 12 pp. 1–39. University of California Press, Berkeley.
- HURD JR., P. D. & LINSLEY, E. G. (1975). The principal *Larrea* bees of southwestern United States (Hymenoptera: Apoidea). *Smithsonian Contributions to Zoology* **193**, 1–74.

- HURD JR., P. D. & POWELL, J. A. (1958). Observations on the nesting habits of *Colletes stephensi* Timberlake. *The Pan-Pacific Entomologist* **34**, 147–153.
- JANDER, U. & JANDER, R. (2002). Allometry and resolution of bee eyes (Apoidea). *Arthropod structure and Development* **30**, 179–193.
- JANZEN, D. H. (1964). Notes on the behavior of four subspecies of the carpenter bees *Xylocopa tabanaformis* in Mexico. *Annals of the Entomological Society of America* **57**, 296–301.
- JANZEN, D. H. (1968). Notes on nesting and foraging behavior of *Megalopta* in Costa Rica. *Journal of the Kansas Entomological Society* **41**, 342–350.
- JØRGENSEN, P. (1912). Beitrag zur biologie einiger südamerikanischer bienen. *Zeitschr Wissensch Insektenbiologie* **8**, 268–271.
- KAJOBE, R. (2007). Pollen foraging by *Apis mellifera* and stingless bees *Meliponula bocandei* and *Meliponula nebulata* in Bwindi Impenetrable National Park, Uganda. *African Journal of Ecology* **45**, 265–274.
- KAPUSTJANSKIJ A., STREINZER M., PAULUS H. F., SPAETHE J. (2007). Bigger is better: implications of body size for flight ability under different light conditions and the evolution of alloethism in bumblebees. *Functional Ecology* **207**, 1130–1136.
- KATO, M. (2006). Ecology of traplining bees and understory pollinators. In *Pollination ecology and the rain forest. Sarawak Studies* (eds D. W. Roubik, S. Sakai, A. A. Hamid Karim), pp. 128–133, *Ecological Studies* **174**, 128–133.
- KAWADA, H., TATSUTA, H., ARIKAWA, K. & TAKAGI, M. (2006). Comparative study on the relationship between photoperiodic host-seeking behavioral patterns and the eye parameters of mosquitoes. *Journal of Insect Physiology* **52**, 67–75.
- KELBER, A., WARRANT, E. J., PFAFF, M., WALLEN, R., THEOBALD, J., WCISLO, W. T. & RAGUSO, R. A. (2006). Light intensity limits foraging activity in nocturnal and crepuscular bees. *Behavioral Ecology* **17**, 63–72.
- KERFOOT, W. B. (1967a). Correlation between ocellar size and the foraging activities of bees (Hymenoptera: Apoidea). *American Naturalist* **101**, 65–70.
- KERFOOT, W. B. (1967b). Nest architecture and associated behavior of the nocturnal bee, *Sphecodogastra texana* (Hymenoptera: Halictidae). *Journal of the Kansas Entomological Society* **40**, 84–93.
- KERFOOT, W. B. (1967c). The lunar periodicity of *Sphecodogastra texana*, a nocturnal bee (Hymenoptera: Halictidae). *Animal Behaviour* **15**, 479–486.
- KIRCHNER, W. H., DRELLER, C., GRASSER, A. & BAIDYA, D. (1996). Time of drone flight of *Apis laboriosa* Smith in Nepal. *Apidologie* **27**, 331–339.
- KNERER, G. & MACKAY, P. (1969). Bionomic notes on the solitary *Erylaeus oenotherae* (Stevens) (Hymenoptera: Halictidae), a matinal summer bee visiting cultivated Onagraceae. *Canadian Journal of Zoology* **47**, 289–294.
- KOENIGER, N. & KOENIGER, G. (2000). Reproductive isolation among species of the genus *Apis*. *Apidologie* **31**, 313–339.
- KOENIGER, N., KOENIGER, G., TINGEK, S., KELIFU, A. & MARDAN, M. (1994). Drones of *Apis dorsata* Fabricius, 1793 congregate under the canopy of tall emergent trees in Borneo. *Apidologie* **25**, 249–264.
- LABERGE, W. E. (1992). New records for *Agapanthinus callophila* (Hymenoptera: Anthophoridae), a bee rare in collections. *Entomological News* **103**, 210–211.
- LABERGE, W. E. & HURD JR., P. D. (1965). A new subgenus and species of matinal *Andrena* from flowers of *Sicyos* (Cucurbitaceae) in Mexico. *The Pan-Pacific Entomologist* **41**, 186–193.
- LABERGE, W. E. & THORP, R. W. (2005). A revision of the bees of the genus *Andrena* of the Western hemisphere. Part XIV Subgenus *Onagrarendra*. *Illinois Natural History Survey Bulletin* **37**, 1–10.
- LAMARCK, J. -B. (1809). *Zoological Philosophy* (1984 re-print). University of Chicago Press, Chicago.
- LAND, M. F., GIBSON, G., HORWOOD, J. & ZEIL, J. (1999). Fundamental differences in the optical structure of the eyes of nocturnal and diurnal mosquitoes. *Journal of Comparative Physiology A* **185**, 91–103.
- LEWONTIN, R. C. (1983). The organism as the subject and object of evolution. *Scientia* **118**, 63–82.
- LEWONTIN, R. C. (2000). *The Triple Helix*. Harvard University Press, Cambridge.
- LINSLEY, E. G. (1958). The ecology of solitary bees. *Hilgardia* **27**, 543–599.
- LINSLEY, E. G. (1960). Observations on some matinal bees at flowers of *Cucurbita*, *Ipomoea*, and *Datura* in desert areas of New Mexico and southeastern Arizona. *Journal of the New York Entomological Society* **68**, 13–20.
- LINSLEY, E. G. (1962). The colletid *Ptiloglossa arizonensis* Timberlake, a matinal pollinator of *Solanum*. *The Pan-Pacific Entomologist* **38**, 75–82.
- LINSLEY, E. G. (1978). Temporal patterns of flower visitation by solitary bees, with particular reference to the southwestern United States. *Journal of the Kansas Entomological Society* **51**, 531–46.
- LINSLEY, E. G. & CAZIER, M. A. (1970). Some competitive relationships among matinal and late afternoon foraging activities of caupolicanine bees in southeastern Arizona (Hymenoptera, Colletidae). *Journal of the Kansas Entomological Society* **43**, 251–261.
- LINSLEY, E. G. & CAZIER, M. A. (1972). Diurnal and seasonal behavior patterns among adults of *Protophaga gloriosa*. *American Museum Novitates* **2509**, 1–25.
- LINSLEY, E. G., & HURD, JR. P. D. (1959). Ethological observations on some bees of south-eastern Arizona and New Mexico. *Entomological News* **70**, 63–68.
- LINSLEY, E. G., MCSWAIN, J. W. & RAVEN, P. H. (1963). Comparative behavior of bees and Onagraceae II. *Oenothera* bees of the Great Basin. *University of California Publications in Entomology* **33**, 25–58.
- LINSLEY, E. G., MCSWAIN, J. W. & RAVEN, P. H. (1964). Comparative behavior of bees and Onagraceae III. *Oenothera* bees of the Mojave Desert, California. *University of California Publications in Entomology* **33**, 59–98.
- LINSLEY, E. G., MCSWAIN, J. W. & SMITH R. F. (1956). Biological observation on *Xenoglossa fulva* Smith with some generalizations on biological characters of other Eucerine bees (Hymenoptera: Anthophoridae). *Bulletin of the Southern California Academy of Sciences* **54**, 128–141.
- LISTABARTH, C. (1996). Pollination of *Bactris* by *Phyllotrox* and *Epurea*. Implications of the palm breeding beetles on pollination at the community level. *Biotropica* **28**, 69–81.
- LUCKOW M. & HOPKINS, H. C. F. (1995). A cladistic analysis of *Parkia* (Leguminosae: Mimosoideae). *American Journal of Botany* **82**, 1300–1320.
- LUTZ, F. E. (1931). Light as a factor in controlling the start of daily activity of a wren and stingless bees. *American Museum Novitates* **469**, 1–9.
- LYTHGOE, J. N. (1979). *The Ecology of Vision*. Oxford University Press, New York.
- MAA, T. C. (1953). An inquiry into the systematics of the tribus Apidini or honeybees, (Hymenoptera). *Treubia* **21**, 525–640.

- MADDISON, W. O. (1990). A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? *Evolution* **44**, 539–557.
- MARSHALL, A. (1983). Bats, flowers and fruit: evolutionary relationships in the Old World. *Biological journal of the Linnean Society* **20**, 115–135.
- MARTIN, G., ROJAS, L. M., RAMIREZ, Y. & MCNEIL, R. (2004). The eyes of oilbirds (*Steatornis caripensis*): pushing at the limits of sensitivity. *Naturwissenschaften* **91**, 26–29.
- MAYR, E. (1958). Behavior and systematics. In *Behavior and Evolution* (eds. A. Roe, G. C. Simpson), pp. 341–62. Yale University Press, New Haven.
- MAYR, E. (1960). The emergence of evolutionary novelties. In *Evolution after Darwin, Volume 1. The Evolution of Life* (ed. S. Tax), pp. 349–80. University of Chicago Press, Chicago.
- MCÉVOY, M. V. & UNDERWOOD, B. A. (1988). The drone and species status of the Himalayan honey bee, *Apis laboriosa* (Hymenoptera: Apidae). *Journal of the Kansas Entomological Society* **61**, 246–248.
- MCGINLEY, R. J. (1986). Studies of Halictinae (Apoidea: Halictidae) I: Revision of New World *Lasioglossum* Curtis. *Smithsonian Contributions to Zoology* **429**, 1–294.
- MCGINLEY, R. J. (2003). Studies of Halictinae (Apoidea: Halictidae), II: Revision of *Sphcodogastra* Ashmead, floral specialists of Onagraceae. *Smithsonian Contribution to Zoology* **610**, 1–55.
- MENZI, U. (1987). Visual adaptation in nocturnal and diurnal ants. *Journal of Comparative Physiology A* **160**, 11–21.
- MICHENER, C. D. (1947). Some observations on *Lasioglossum (Hemihalictus) lustrans* (Hymenoptera, Halictidae). *Journal of the New York Entomological Society* **55**, 49–50.
- MICHENER, C. D. (1954). Bees of Panamá. *Bulletin of the American Museum of Natural History* **104**, 1–176.
- MICHENER, C. D. (1966). The classification of the Diphaglossinae and North American species of the genus *Caupolicana* (Hymenoptera, Colletidae). *The University of Kansas Science Bulletin* **46**, 717–751.
- MICHENER, C. D. (1986). A review of the tribes Diphaglossini and Dissoglottini (Hymenoptera, Colletidae). *The University of Kansas Science Bulletin* **53**, 183–214.
- MICHENER, C. D. (2007). *The Bees of the World*. Johns Hopkins University Press, Baltimore.
- MICHENER, C. D. & LANGE, R. B. (1958). Observations on the behavior of Brazilian halictid bees III. *University Kansas Science Bulletin* **39**, 437–505.
- MICHENER, C. D., MCGINLEY, R. J. & DANFORTH, B. N. (1994). *The Bee Genera of North and Central America (Hymenoptera: Apoidea)*. Smithsonian Institution Press, Washington.
- MICHENER, C. D. & WILLE, A. (1961). The bionomics of a primitively social bee, *Lasioglossum inconspicuum*. *University of Kansas Science Bulletin* **42**, 1123–1202.
- MINCKLEY, R. L. (1998). A cladistic analysis and classification of the subgenera and genera of large carpenter bees, Tribe Xylocopini. *Scientific Papers, Natural History Museum, University of Kansas* **9**, 1–47.
- MINCKLEY, R. L., CANE, J. H. & KERVIN, L. (2000). Origins and ecological consequences of pollen specialization among desert bees. *Proceedings of the Royal Society of London (Series B)* **267**, 1–7.
- MINCKLEY, R. L., WCISLO, W. T., YANEGA, D. A. & BUCHMANN, S. L. (1994). Behavior and phenology of a specialist bee (*Dieunomia*) and sunflower (*Helianthus*) pollen availability. *Ecology* **75**, 1406–1419.
- MIZUNAMI, M. (1994). Information processing in the insect ocellar system: comparative approaches to the evolution of visual processing and neural circuits. *Advances in Insect Physiology* **25**, 151–265.
- MOMOSE, K., YUMOTO, T., NAGAMITSU, T., KATO, M., NAGAMASU, H., SAKAI, S., HARRISON, R. D., ITOKA, T., HAMID, A. A. & INOUE, T. (1998). Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. I. Characteristics of the plant-pollinator community in a lowland dipterocarp forest. *American Journal of Botany* **85**, 1477–1501.
- MOORE, D. (2001). Honey bee circadian clocks: behavioral control from individual workers to whole-colony rhythms. *Journal of Insect Physiology* **47**, 843–857.
- MOSER, J. C., REEVE, J. D., BENTO, J. M. S., DELLA LUCIA, T. M. C., CAMERON, R. S. & HECK, N. M. (2004). Eye size and behavior of day- and night-flying leafcutting ant alates. *Journal of Zoology, London* **264**, 69–75.
- MOUGEOT, F. & BRETAGNOLLE, V. (2000). Predation risk and moonlight avoidance in nocturnal seabirds. *Journal of Avian Biology* **31**, 376–386.
- MOURE, J. S. (1958). On the species of *Megalopta* described by F. Smith (Hymenoptera, Apoidea). *Journal of the New York Entomological Society* **66**, 179–190.
- MOURE, J. S. & HURD, P. D. JR. (1987). *An Annotated Catalog of the Halictid Bees of the Western Hemisphere (Hymenoptera: Halictidae)*. Smithsonian Institution Press, Washington D.C.
- MOURE, J. S., URBAN, D., & MELO, G. A. R. (2007). *Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region*. Sociedade Brasileira de Entomologia, Curitiba, Brasil.
- NIVEN, J. E. & LAUGHLIN, S. B. (2008). Energy limitation as a selective pressure on the evolution of sensory systems. *Journal of Experimental Biology* **211**, 1972–1804.
- ODLING-SMEE, F. J., LALAND, K. N. & FELDMAN, M. W. (2003). *Niche Construction: The Neglected Process in Evolution*. Princeton University Press, Princeton.
- OSTER, H., AVIVI, A., JOEL, A., ALBRECHT, U. & NEVO, E. (2002). A switch from diurnal to nocturnal activity in *S. eherenbergi* is accompanied by an uncoupling of light input and the circadian clock. *Current Biology* **12**, 1919–1922.
- OTIS, G. W. (1996). Distributions of recently recognized species of honey bees (Hymenoptera: Apidae: *Apis*) in Asia. *Journal of the Kansas Entomological Society* **69** (issue 4, supplement no. 2), 311–333.
- PARK, O. (1940). Nocturnalism – The development of a problem. *Ecological Monographs* **10**, 486–536.
- PEREBOOM, J. J. M. & BIESMEIJER, J. C. (2003). Thermal constraints for stingless bee foragers: the importance of body size and coloration. *Oecologia* **137**, 42–50.
- PRUM, R. O. (1998). Sexual selection and the evolution of mechanical sound production in manakins (Aves: Pipridae). *Animal Behaviour* **55**, 977–994.
- RAU, P. (1933). *The Jungle Bees and Wasps of Barro Colorado Island*. Von Hoffman Press, St. Louis.
- READ, A. F. & NEE, S. (1995). Inference from binary comparative data. *Journal of Theoretical Biology* **173**, 99–108.
- ROBERTS, R. B. (1969). Biology of the bee genus *Agapostemon* (Hymenoptera: Halictidae). *The University of Kansas Science Bulletin* **48**, 689–719.
- ROBERTS, R. B. (1971). Biology of the crepuscular bee *Ptiloglossa guinnæ* n. sp. with notes on associated bee, mites and yeasts. *Journal of the Kansas Entomological Society* **44**, 283–294.
- ROBERTS, R. B. (1972). Revision of the bee genus *Agapostemon* (Hymenoptera: Halictidae). *The University of Kansas Science Bulletin* **49**, 437–590.

- ROBERTS, R. B. & BROOKS, R. W. (1987). Agapostemonine bees of Mesoamerica (Hymenoptera: Halictidae). *The University of Kansas Science Bulletin* **53**, 357–392.
- ROSS, C. F. & KIRK, E. C. (2007). Evolution of eye size and shape in primates. *Journal of Human Evolution* **52**, 294–313.
- ROUBIK, D. W. (1989). *Ecology and natural history of tropical bees*. Cambridge University Press, New York.
- ROUBIK, D. W. (2001). Ups and downs in pollinator populations: when is there a decline? *Conservation Ecology* **5**: 27–55
- ROUBIK, D. W. SAKAGAMI, S. F. & KUDO I. (1985). A note on distribution and nesting of the Himalayan honey bee *Apis laboriosa* Smith (Hymenoptera: Apidae). *Journal of the Kansas Entomological Society* **58**, 746–749.
- ROULSTON, T. H. (1997). Hourly capture of two species of *Megalopta* (Hymenoptera: Apoidea; Halictidae) at black lights in Panama with notes on nocturnal foraging by bees. *Journal of the Kansas Entomological Society* **70**, 189–196.
- ROULSTON, T. H., CANE, J. H. & BUCHMANN S. L. (2000). What governs protein content of pollen: pollinator preferences, pollen-pistil interactions, or phylogeny? *Ecological Monographs* **70**, 617–643.
- ROZEN JR., J. G. (1966). The larvae of Anthophoridae (Hymenoptera, Apoidea). Part 2. The Nomadinae. *American Museum Novitates* **2244**, 1–38.
- ROZEN JR., J. G. (1984). Nesting biology of diploglossine bees (Hymenoptera, Colletidae). *American Museum Novitates* **2786**, 1–33.
- RYDELL, J. & SPEAKMAN, J. R. (1995). Evolution of nocturnality in bats: potential competitors and predators during their early history. *Biological Journal of the Linnean Society* **54**, 183–191.
- SAKAGAMI, S. F. & FUKUDA, H. (1989). Nest founding and nest survival in a eusocial halictine bee, *Lasiglossum duplex*, additional observations. *Researches in Population Ecology* **31**, 139–151.
- SAKAGAMI, S. F., MATSUMURA, T. & ITÔ, K. (1980). *Apis laboriosa* in Himalaya, the little known world largest honeybee (Hymenoptera, Apidae). *Insecta Matsumurana* **19**, 47–77.
- SAKAGAMI, S. F. & MOURE, J. S. (1967). Additional observations on the nesting habits of some Brazilian halictine bees (Hymenoptera, Apoidea). *Mushi* **40**, 119–138.
- SANTOS, L. M., MELO, G. A. R. & SILVEIRA, F. A. (2008). Distribuição geográfica das espécies Brasileiras do gênero *Megalopta* Smith 1853 (Apidae: Halictinae) *Anais do VII Encontro sobre Abelhas, 2008, Ribeirão Preto, SP, Brasil*, p. 738
- SCHROTTKY (1907). A contribution to the knowledge of some South American Hymenoptera, chiefly from Paraguay. Smithsonian Miscellaneous Collection **48**, 259–274.
- SCHWARZ, H. F. (1934). The social bees (Meliponidae) of Barro Colorado Island, Canal Zone. *American Museum Novitates* **731**, 1–23.
- SHASHAR, N., CRONIN, T. W., WOLFE, L. B. & CONDON, M. A. (1998). The polarization of light in a tropical rain forest. *Biotropica* **30**, 275–285.
- SMITH, A. R., WCISLO, W. T. & O'DONNELL, S. (2003). Assured fitness returns favor sociality in a mass-provisioning sweat bee, *Megalopta genalis* (Hymenoptera: Halictidae). *Behavioral Ecology & Sociobiology* **54**, 14–21.
- SMITH, A. R., WCISLO, W. T. & O'DONNELL, S. (2008). Parasites influence body size in the facultatively eusocial bees, *Megalopta* (Hymenoptera: Halictidae): a role in caste determination? *Journal of Insect Behavior* **21**, 394–406.
- SMITH, S. D. & KNAPP, S. (2002). The natural history of reproduction in *Solanum* and *Lycianthes* (Solanaceae) in a subtropical moist forest. *Bulletin of the Natural History Museum London (Botany)* **32**, 125–136.
- SOKAL, R. R. & ROHLF F. J. (1995). *Biometry, Third Edition*. Freeman, New York.
- SOMANATHAN, H. & BORGES, R. M. (2001). Nocturnal pollination by the carpenter bee *Xylocopa tenuiscapa* (Apidae) and the effect of floral display on fruit set of *Heterophagma quadriloculare* (Bignoniaceae) in India. *Biotropica* **33**, 78–89.
- SOMANATHAN, H., BORGES, R. M. & CHAKRAVARTHY, V. S. (2004). Does neighborhood floral display matter? Fruit set in carpenter bee-pollinated *Heterophagma quadriloculare* and beetle-pollinated *Lasiosiphon eriocephalus*. *Biotropica* **36**, 139–147.
- SOMANATHAN, H., BORGES, R. M., WARRANT, E. J. & KELBER, A. (2008). Visual ecology of Indian carpenter bees I: light intensities and flight activity. *Journal of Comparative Physiology A* **194**, 97–107.
- SOMANATHAN, H., KELBER, A., WARRANT, E. J. & BORGES, R. M. (2006). Divided we don't fall: partitioning of time and food resources in a carpenter bee community in India. Proceedings of *The Annual Meeting of the Association for Tropical Biology and Conservation 18-21 July 2006 Kunming, Yunnan, China*. Pp. 62–63.
- SPAETHE, J. & CHITTKA, L. (2003). Interindividual variation of eye optics and single object resolution in bumblebees. *Journal of Experimental Biology* **206**, 3447–3453.
- STEBBINS G. L. (1970). Adaptive radiation of reproductive characteristics in angiosperms, I: pollination mechanisms. *Annual Review of Ecology & Systematics* **1**, 307–326.
- STEVENS, O. A. (1920). Notes on species of *Halictus* visiting evening flowers. *Entomological News* **31**, 35–44.
- THEOBALD, J. C., COATES, M. M., WCISLO, W. T. & WARRANT, E. J. (2007). Flight performance in night-flying sweat bees suffers at low light levels. *Journal of Experimental Biology* **210**, 4034–4042.
- THEOBALD, J. C., GREINER, B., WCISLO, W. T. & WARRANT, E. J. (2006). Visual summation in night-flying sweat bees: a theoretical study. *Vision Research* **46**, 2298–2309.
- THOMAS, R. J., SZÉKELY, T., POWELL, R. F. & CUTHILL, I. C. (2006). Eye size, foraging methods and the timing of foraging in shorebirds. *Functional Ecology* **20**, 157–165.
- THORP, R. W. (1969). Systematics and ecology of bees of the sub-genus *Diandrena*. *University of California Publications in Entomology* **52**, 1–146.
- THORP, R. W. (1979). Structural, behavioral and physiological adaptations of bees (Apoidea) for collecting pollen. *Annals of the Missouri Botanical Garden* **66**, 788–812.
- TIERNEY, S. M., GONZALES-OJEDA, T. & WCISLO, W. (2008a). Biology of a nocturnal bee, *Megalopta atra* (Hymenoptera: Halictidae; Augochlorini), from the Panamanian highlands. *Journal of Natural History* **42**, 1841–1847.
- TIERNEY, S. M., GONZALES-OJEDA, T. & WCISLO, W. (2008b). Nesting Biology and Social Behavior of *Xenochlora* Bees (Hymenoptera: Halictidae: Augochlorini) from Perú. *Journal of the Kansas Entomological Society* **81**, 61–72.
- VESEY-FITZGERALD, D. (1939). Observations on bees (Hymenoptera: Apoidea) in Trinidad, B. W. I. *Proceeding of the Royal Entomological Society of London A* **14**, 107–110.
- WARRANT, E. (2004). Vision in the dimmest habitat on earth. *Journal of Comparative Physiology A* **190**, 765–78.
- WARRANT, E. (2008). Seeing in the dark: vision and visual behaviour in nocturnal bees and wasps. *Journal of Experimental Biology* **211**, 1737–w1746.
- WARRANT, E. J., KELBER, A., GISLÉN, A., GREINER, B., RIBI, W. & WCISLO, W. T. (2004). Nocturnal vision and landmark orientation in a tropical halictid bee. *Current Biology* **14**, 1309–1318.
- WARRANT, E. J., KELBER, A., WALLÉN, R. & WCISLO, W. T. (2006). The physiological optics of ocelli in nocturnal and

- diurnal bees and wasps. *Arthropod Development and Evolution* **35**, 293–305.
- WARRANT, E., POROMBKA, T. & KIRCHNER, W. H. (1996). Neural image enhancement allows honeybees to see at night. *Proceeding of the Royal Society of London B* **263**, 1521–1526.
- WCISLO, W. T. (1989). Behavioral environments and evolutionary change. *Annual Review of Ecology and Systematics* **20**, 137–169.
- WCISLO, W. T. (1992). Nest localization and recognition in a solitary bee, *Lasioglossum (Dialictus) figueresi* Wcislo (Hymenoptera: Halictidae), in relation to sociality. *Ethology* **92**, 108–123.
- WCISLO, W. T. (1996). Rates of parasitism in relation to nest site in bees and wasps (Hymenoptera: Apoidea). *Journal of Insect Behavior* **9**, 643–656.
- WCISLO, W. T., ARNESON, L., ROESCH, K., GONZALEZ, V., SMITH, A. & FERNÁNDEZ, H. (2004). The evolution of Nocturnal behaviour in sweat bees, *Megalopta genalis* and *M. ecuadoria* (Hymenoptera: Halictidae): an escape from competitors and enemies? *Biological Journal of the Linnean Society* **83**, 377–387.
- WCISLO, W. T. & CANE, J. H. (1996). Floral resource utilization by solitary bees (Hymenoptera: Apoidea) and exploitation of their stored foods by natural enemies. *Annual Review of Entomology* **41**, 257–286.
- WEBER, B. H. & DEPEW, D. J. (2003). *Evolution and Learning: The Baldwin Effect Reconsidered*, 341 pp. MIT Press, Cambridge.
- WEST-EBERHARD, M. J. (2003). *Developmental Plasticity and Evolution*, 794 pp. Oxford University Press, New York.
- WILLMER, P. G. & STONE, G. N. (1997). Temperature and water relations in desert bees. *Journal of Thermal biology* **22**, 453–465.
- WOLDA, H. & ROUBIK, D. W. (1986). Nocturnal bee abundance and seasonal bee activity in a Panamanian forest. *Ecology* **67**, 426–433.
- WRIGHT, S. J. (2005). The influence of the El Niño southern oscillation on tropical forests. In *Rain Forests: Past, Present and Future* (eds E. Birmingham, C. Dick & C. Moritz), pp. 295–310. University Chicago Press, Chicago.
- WRIGHT, S. J. & CALDERÓN, O. (1995). Phylogenetic patterns among Tropical Flowering Phenologies. *The Journal of Ecology* **83**, 937–948.
- WRIGHT, S. J. & CALDERÓN, O. (2006). Seasonal, El Niño and longer term changes in flower and seed production in a moist tropical forest. *Ecology Letters* **9**, 35–44.
- WRIGHT, S. J., CARRASCO, C., CALDERÓN, O. & PATON, S. (1999). The El Niño Southern oscillation, variable fruit production, and famine in a tropical forest. *Ecology* **80**, 1632–1647.
- YACK, J. E., JOHNSON, S. E., BROWN, S. G. & WARRANT, E. J. (2007). The eyes of *Macrosoma* sp. (Lepidoptera: Hedyloidea): A nocturnal butterfly with superposition optics. *Arthropod Structure and Development* **36**, 11–22.
- YUAN, Q., METTERVILLE, D., BRISCOE, A. D. & REPPERT, S. M. (2007). Insect cryptochromes: Gene duplication and loss define diverse ways to construct insect circadian clocks. *Molecular Biology and Evolution* **24**, 948–955.
- YOKOYAMA S., & R. YOKOYAMA. (1996). Evolution of photoreceptor cells and visual pigments. *Annual Review of Ecology & Systematics* **27**, 543–567.
- ZAVORTINK, T. J. & LABERGE, W. E. (1976). Bees of the genus *Martinapis* Cockrell in North America. *The Wasmann Journal of Biology* **34**, 119–145.
- ZAYED A., & PACKER L. (2007). The population genetics of a solitary oligolectic sweat bee, *Lasioglossum (Sphecodogastra) oenotherae* (Hymenoptera: Halictidae). *Heredity* **99**, 397–405.