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REVIEW

Diel behavior in moths and butterflies: a synthesis of data illuminates the evolution of temporal activity

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Abstract Lepidoptera (butterflies and moths) are one of the most taxonomically diverse insect orders with nearly 160,000 described species. They have been studied extensively for centuries and are found on nearly all continents and in many environments. It is often assumed that adult butterflies are strictly diurnal and adult moths are strictly nocturnal, but there are many exceptions. Despite the broad interest in butterflies and moths, a comprehensive review of diel (day-night) activity has not been conducted. Here, we synthesize existing data on diel activity in Lepidoptera, trace its evolutionary history on a phylogeny, and show where gaps lie in our knowledge. Diurnality was likely the ancestral condition in Lepidoptera, the ancestral heteroneuran was likely nocturnal, and more than 40 transitions to diurnality subsequently occurred. Using species diversity estimates across the order, we predict that roughly 75-85% of Lepidoptera are nocturnal. We also define the three frequently used terms for activity in animals (diurnal, nocturnal, crepuscular), and show that literature on the activity of micro-moths is significantly lacking. Ecological factors leading to nocturnality/diurnality is a compelling area of research and should be the focus of future studies.

Keywords Crepuscular · Day-flying · Diurnal · Flight time · Lepidoptera · Night-flying · Nocturnal

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Introduction

Lepidoptera (butterflies and moths) is one of the most taxonomically diverse insect orders with approximately 160,000 described species (van Nieukerken et al. 2011). They have been studied extensively for centuries and occupy nearly all continents and environments (Scoble 1992). Adult butterflies are often thought to be active strictly during the day, but some butterflies (e.g., Hedylidae) are predominantly nocturnal (Scoble 1986). Similarly, adult moths are often thought to be nocturnal, but many lineages are known to be day-flying (Scoble 1992). Some species differ significantly in diel (day-night) activity time based on sex (Franclemont 1973; Evans 1978; Tuskes et al. 1996), and there are a few cases where species are strictly crepuscular (i.e., they are only active during twilight hours (Kan et al. 2002)). While there is a large amount of existing literature published in field guides and other sources, many reports exist only as personal observations or remain hidden on museum specimen labels. Despite being one of the most popular and charismatic insect groups, our understanding of diel activity in butterflies and moths is relatively poor, and a comprehensive review of diel activity has not been conducted.

Phylogenetic relationships of Lepidoptera have been studied extensively, and until recently, there was significant contention about major relationships, especially among superfamilies (Mitter et al. 2017, and references therein). Some

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authors have assumed that the ancestral condition for adult Lepidoptera was nocturnal (Yack and Fullard 2000; Feuda et al. 2016), though others have suggested otherwise (Kozlov et al. 2007). Fullard and Napoleone (2001) proposed that the earliest ancestral lepidopteran flew both during the day and at night. However, to our knowledge, no one has formally examined the evolution of activity time across Lepidoptera. Here, we use one of the most taxonomically well-sampled phylogenies of Lepidoptera (Regier et al. 2013) to test the hypothesis that the ancestral lepidopteran was nocturnal. We do not discuss the behavior of immature stages here, although larvae can exhibit different diel activity than adults (e.g., Berger and Gotthard 2008). We also define the three frequently used terms for activity in insects (diurnal, nocturnal, crepuscular), review existing literature on diel activity in Lepidoptera, and examine how diel activity has evolved across the order.

Materials and methods

Data sampling

Diel activity data was compiled by searching all available resources (see Table S1 for these data and a list of references). We categorized taxa into one of the three activity periods—diurnal, nocturnal, or crepuscular (Table S1; for a definition of these terms, see section below). When species with multiple states were found, the state that was most biologically realistic was chosen, based on known natural history of closely related lineages. A species was considered active if adults had been observed feeding, mating, or flying (or crawling, in the case of brachypterous females). We also characterized diel activity for an exemplar set of Trichoptera, in order to infer the state of the ancestral Lepidoptera (see below). While there is variation in diel activity within Trichoptera, caddisflies are predominantly crepuscular; this is thought to be the ancestral condition in the order (Harris 1971; Wiggins 1998).

To examine the evolution of diel activity, we utilized a published phylogeny of Regier et al. (2013). We chose the Regier et al. phylogeny because it is one of the most taxon-rich available phylogenies of Lepidoptera to date. Because many relationships among superfamilies remain poorly supported in the Regier et al. phylogeny, we applied a constrained backbone derived from Kawahara and Breinholt (2014) and Bazinet et al. (2017), two studies that relied on a much larger RNA-Seq character dataset and resulted in well-resolved RNA-Seq phylogenies. The chimeric topological constraint phylogeny was constructed in Newick format, without branch lengths, and contained family-level relationships from the topologies in those two studies (Fig. 2 from Kawahara and Breinholt (2014) and Fig. 2 from Bazinet et al. (2017)); there were no differences in family-level relationships between these two phylogenies, so the combined constraint tree was created without conflict (Supp. Tree 1). To create a proper consensus, tips were given family member names that matched the taxa in the dataset of Regier et al. (2013). Additional taxa were pruned from the constraint phylogeny so that only one representative per family was utilized, corresponding to 32 families (Supp. Tree 1).

Phylogenetic inference employing the topological constraint was carried out using maximum likelihood in RAxML v8.2 (Stamatakis 2014), under a GTRGAMMA model of evolution with 100 bootstraps for node support. Analyses were conducted on the following datasets: (1) all nucleotide positions (nt123) from Regier et al. (2013), (2) all nucleotide positions excluding synonymous signal (nt123_degen1) of Regier et al., and (3) partitioning by site on the Regier et al. “nt123” dataset. All trees can be found in the supplementary tree files (Supp. Trees 2–5).

We reconstructed ancestral character states of adult diel activity (i.e., nocturnal, crepuscular, diurnal, and all states) on the ML constrained trees from the three analyses (degen1, nt123, nt123 partitioned). We generated 10,000 stochastic maps for each tree in SIMMAP, which is part of the R package “phytools” (Revell 2012). Stochastic character mapping is a Bayesian approach that is more robust to parsimony character state reconstruction (Bollback 2006). It is thought to be more powerful than other likelihood approaches because it allows for changes to occur along branches, and permits the assessment of uncertainty in character history due to topology and branch lengths (Revell 2013). SIMMAP does not allow for missing or unknown data, therefore all tips were coded with a discrete, unordered character state (as defined above). Other methodologies that are able to utilize missing data (i.e., utilized datasets with large amounts of unknown states), led to highly divergent ancestral state reconstructions (i.e., ancestral states were inferred seemingly randomly across the phylogeny), and we therefore do not present these results.

For species in the Regier et al. (2013) trees that lacked published diel activity data, we utilized records from online sources, consultations with lepidopterists, and collection time data from pinned museum specimens. However, because not all species had activity data, and because the time of collection does not indicate that the insect was active at that time of day, we used available diel activity data from closely related taxa in order to make the necessary character-state assignments (see Table S1). Although there can be biases to this approach, we believe we have assembled the best-possible dataset of diel activity with the available material, we caution that some character scoring will need to be updated, as more data are collected.

Definition of terms

The definition of the three categories of diel activity has remained ambiguous and has not been consistently applied across relevant literature. In the broad sense, diurnality implies activity during the day, nocturnality implies activity at night, and crepuscular activity occurs during the twilight hours in between (i.e., dawn and dusk). However, when discussing activity times of crepuscular organisms, it is necessary to formally establish temporal boundaries of twilight that can be consistently applied across all latitudes. Much of the recent research on crepuscular insects (e.g., Kelber et al. 2006; Narendra et al. 2010; Meiswinkel and Elbers 2016) uses the definition of astronomical twilight adopted by the US Naval Observatory (United States Naval Oceanography Portal 2011) and other governmental organizations. In the morning, astronomical twilight begins when the sun's center is 18° below the horizon, and ends at sunrise. Evening twilight begins at sunset and ends when the sun's center is 18° below the horizon. At 18°, the sun "no longer contributes any significant amount of light to the sky" (Kelber et al. 2006). Although this definition is somewhat biased by the visual acuity of humans, we choose to use it here because it is likely the definition implemented in historical observations of Lepidoptera activity, since it only requires collectors to observe the presence or absence of sunlight in the sky.

Diel activity in Lepidoptera: a synthesis

Below, we review diel activity in Lepidoptera and present a brief synopsis of diel activity in Trichoptera. Lineages are discussed in phylogenetic order, from earliest-diverging to latest-diverging, according to our ancestral state reconstruction on the Regier et al. (2013) topologically constrained nt123 partitioned dataset. We show ancestral state reconstructions on this tree, as it had the best overall node support and most realistic topology among the three ML trees (see Supp. Trees 3 and 4 for the two other topologies and their ancestral state reconstructions). Figure 1 shows a simplified tree of the ancestral state reconstructions; species-level reconstructions on the 483-species tree can be found in Fig. S1. Images of exemplar Lepidoptera species from different diel clades are shown in Fig. 1.

Trichoptera

The sister group relationship of Lepidoptera to Trichoptera is well-established (Hennig 1981; Whiting et al. 1997; Misof et al. 2014). Adult Trichoptera generally exhibit cryptic coloration and are thought to be predominantly crepuscular, but there are a few exceptions (Wiggins 1998). Diurnal adults are generally known from species found in temperate and arctic latitudes (Wells 1990; Ward 1995). It is conceivable that low night temperatures may make nocturnal flight more difficult for some species in colder climates, but this has not been thoroughly studied. Large synchronized emergences and brightly colored adults are known for many diurnal species; these traits are suspected to be anti-predation adaptations (Petersson 1989; Wiggins 2015). Few studies have delimited between crepuscular and nocturnal flight activity times in Trichoptera, but Harris (1971) found a peak in activity during the hour beginning at twilight. We believe this is sufficient evidence to treat Trichoptera as a crepuscular order, albeit with significant amounts of nocturnality in multiple independent lineages.

Non-ditrysian moths

The non-ditrysian Lepidoptera lineages appear to undergo multiple shifts in diel activity. The traditional morphology-based phylogeny placed the largely diurnal Micropterigoidea sister to all other Lepidoptera, with the nocturnal, monotypic superfamily Agathiphagoidea subsequently placed sister to the remaining Lepidoptera (Kristensen and Skalski 1998). Although this topology had been challenged in some analyses (e.g., Regier et al. 2015a), it is strongly supported by the most recent phylotranscriptomic analysis (Bazinet et al. 2017), which suggests a high probability of the immediate ancestor of Lepidoptera as diurnal (Figs. 1 and S1).

The remaining non-heteroneuran taxa (including the recently discovered family Aenigmatineidae, not present in our analysis) are mainly diurnal (Kristensen et al. 2015). The exceptions are the superfamilies Lophocoronoidea and Hepialoidea. The former is crepuscular with some species occasionally also observed early in the night (Nielsen and Kristensen 1996), and the latter consists of mostly crepuscular species, with some nocturnal or diurnal exceptions (Kristensen 1998). Hepialoidea historically contained multiple species-depauperate families that are now all included in the single family Hepialidae (Regier et al. 2015a); some of the diurnal taxa were originally placed in these now-invalid families (e.g., Palaeosetidae (Regier et al. 2015a) and Prototheoridae (Davis 2001)). The diurnal genus *Oxygioses* is sister to all other hepialoids in our analysis, so the ancestral hepialoid is posited to have been diurnal (Fig. 1), with a shift to crepuscularity occurring shortly thereafter (Fig. S1). *Oxygioses* was originally placed in Palaeosetidae, so our analysis suggests that its separation from Hepialidae sensu stricto may have been justified. However, further taxon sampling would be required to make a more conclusive determination.

Our analysis indicates a ~ 64% probability that the ancestral heteroneuran was nocturnal, suggesting another shift in diel activity (Node 3, Fig. 1). Nepticuloidea, which contains the families Nepticulidae and Opostegidae, and is sister to all other Heteroneura, appears to be ancestrally nocturnal

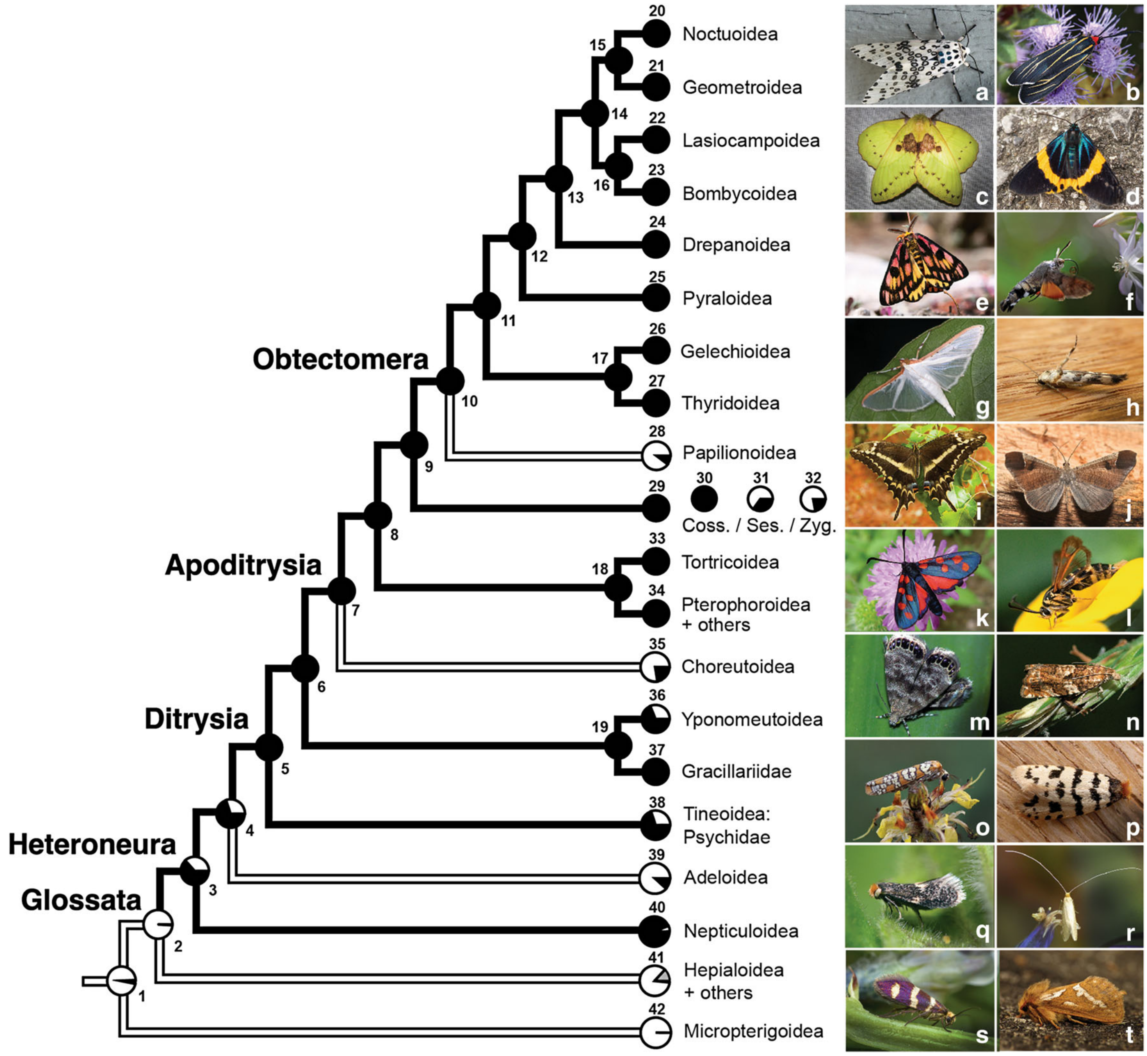

Fig. 1 Simplified tree showing the evolution of diel activity in adult Lepidoptera, inferred from the "nt123_partitioned" dataset of Regier et al. (2013) with an RNA-Seq based topological constraint from Kawahara and Breinholt (2014) and Bazinet et al. (2017). This tree excludes some of the nodes and less diverse lineages in Lepidoptera; the complete nt123_partitioned phylogeny with all taxa in the dataset and all estimations of ancestral state probabilities can be found in Fig. S1. Colors of branches and pies: black = nocturnal, gray = crepuscular, white = diurnal. Most tips represent superfamily-level clades; the exceptions are tips at nodes 31, 32, 37, and 38, which represent families. Images of Lepidoptera shown: **a** *Hypercompe scribonia* (Noctuoidea: Erebidae), nocturnal. **b** *Ctenucha* sp. (Noctuoidea: Erebidae), diurnal. **c** *Trabala ganesha* (Lasiocampoidea: Lasiocampidae), nocturnal. **d** *Milionia basalis* (Geometroidea: Geometridae), diurnal. **e** *Hemileuca eglanterina* (Bombycoidea: Saturniidae), diurnal. **f** *Macroglossum stellatarum* (Bombycoidea: Sphingidae), diurnal. **g** *Palpita isoscelalis* (Pyraloidea: Crambidae), nocturnal. **h** *Stathmopoda melanochra* (Gelechioidea: Stathmopodidae), diurnal. **i** *Papilio aristodemus* (Papilionoidea: Papilionidae), diurnal. **j** *Macrosoma* sp. (Papilionoidea: Hedylidae), nocturnal. **k** *Zygaena transalpina* (Zygaenoidea: Zygaenidae), diurnal. **l** *Carmenta arizonae* (Sesioidea: Sesiidae), diurnal. **m** *Brenthia* sp. (Choreutoidea: Choreutidae), diurnal. **n** *Epinotia abbreviana* (Tortricoidea: Tortricidae), nocturnal. **o** *Atteva aurea* (Yponomeutoidea: Attevidae), all. **p** *Iphierga* sp. (Tineoidea: Psychidae), nocturnal. **q** *Ectoedemia albifasciella* (Nepticuloidea: Nepticulidae), all. **r** *Nematopogon swammerdamella* (Adeloidea: Adelidae), diurnal. **s** *Micropterix aureatella* (Micropterigoidea: Micropterigidae), diurnal. **t** *Korscheltellus lupulina* (Hepialoidea: Hepialidae), crepuscular. See Table S2 for image attributions; see Table S4 for specific node probabilities.

(Figs. 1 and S1) but extant taxa exhibit variable diel activity. Some species of Nepticulidae are both diurnal and nocturnal, though relatively little is known about activity of the family as a whole, in part because these are extremely small moths (van Nieukerken, personal communication). Opostegidae are mostly nocturnal, with some diurnal and crepuscular species reported by Davis (1989) and Davis and Stonis (2007). Incurvariina appears to include another shift, with the nocturnal monotypic Andesianoidea being placed as the sister group to the mostly diurnal Adeloidea (Fig. S1). Within the Adeloidea, at least one species of yucca moth (Prodoxidae) is nocturnal (Pellmyr 1999), though most obligate yucca pollinators are diurnal (Pellmyr and Balcázar-Lara 2000). Both nocturnal and crepuscular behavior has been reported in the adelid genus *Nematopogon* (Regier et al. 2015a).

The remaining non-ditrysian superfamilies, Tischerioidea and Palaephatoidea, form a monophyletic group with the Ditrysia; this clade was recently named Euheteroneura (Regier et al. 2015a). Palaephatoidea are thought to be primarily diurnal (Heppner 2008g), though Nielsen (1987) reported an apparent shift in *Azaleodes*, since all species in that genus are nocturnally active and fly to lights. Davis (1986) mentions additional genera that he implies are nocturnal (e.g., *Metaphatus*, *Palaephatus*) because they have larger eyes and are more attracted to ultraviolet light, relative to known diurnal genera. Tischerioidea are currently believed to be nocturnal (Fasoranti 1983; S. Kobayashi, personal communication).

Tineoidea

Tineoidea includes the families Tineidae, Dryadaulidae, Eriocottidae, Meessiidae, and Psychidae, with the Dryadaulidae and Meessiidae having been recently given family-level status (Regier et al. 2015b). Many species of Tineoidea are nocturnal, but records of diurnal and crepuscular activity are also common, making it difficult to accurately summarize activity times within this superfamily. Robinson and Nielsen (1993) state that most Tineidae are nocturnal or crepuscular, but note that there are several exceptions. Diurnality is commonly observed in the families Psychidae (Rhainds et al. 2009) (Fig. 1) and Dryadaulidae, which are all currently placed in the single genus *Dryadaula* and are active during the day and night (Powell and Opler 2009; Kawahara et al. 2011a). Davis (1990) noted that the life histories of most Eriocottidae are unknown, though the genus *Crepidochares* has only been collected at ultraviolet light, indicating probable nocturnality. Likewise, little information is available about the flight activity of Meessiidae, although Powell and Opler (2009) report one species of *Homosetia* as nocturnal.

Yponomeutoidea and Gracillarioidea

The most recent classification of the Yponomeutoidea (Sohn et al. 2013) includes 11 families within the superfamily, with at least six families containing diurnal species. The families Glyphipterigidae and Heliodinidae are predominantly diurnal, as well as the subfamily Ochsenheimeriinae of the Ypsolophidae (Dugdale et al. 1998). Flight activity records are limited for the Attevidae, which includes a single genus, *Atteva*. However, Powell and Opler (2009) noted that, while *Atteva aurea* is attracted to lights, this species has also been observed on flowers during the day. Lyonetiidae contains diurnal species (Michereff et al. 2007; A. Sourakov, personal communication), with crepuscular activity reported in at least one species of the genus *Lyonetia* (Sekita 2002). The invasive diamondback moth, *Plutella xylostella* (Plutellidae), is commonly observed flying at night and at dusk, though it is also diurnally active (Goodwin and Danthanarayana 1984; Idris and Zainal-Abidin 2011). Australian populations of *P. xylostella* exhibited sexual variation in flight activity: male flight periods were approximately 19-h, longer than the 16-h flight periods of females (Goodwin and Danthanarayana 1984).

Gracillarioidea consists of the species-rich family Gracillariidae, as well as the less speciose Bucculatricidae and Roeslerstammiidae (Kawahara et al. 2011b, 2017). The latter two families are diurnal, but diel activity of Gracillariidae is more variable and less known due to an absence of data for most of its 2000 described species (De Prins and De Prins 2017). Many species are nocturnal, particularly in Afrotropical regions (J. De Prins, personal communication) but there are also numerous examples of diurnal taxa. For example, the Hawaiian *Philodoria* includes ~30 described species (Johns et al. 2016) of which some are diurnal, nocturnal, or both (C. Johns, personal communication), indicating that diel activity can vary within and between gracillariid genera.

Choreutoidea

Choreutoidea appears to be predominantly diurnal, except for some species that have been collected at lights (Rota and Miller 2013). Diurnal Choreutidae often have bright wing coloration and are thought to be associated with aposematism. The diurnal *Brenthia* has been shown to mimic predatory jumping spiders (Rota and Wagner 2006), and it is likely that this form of Batesian mimicry is also present in other choreutid genera.

The Millieriidae was once placed in Choreutoidea and treated as a subfamily of Choreutidae (Rota and Kristensen 2011). However, it has since been found to be polyphyletic, unrelated to Choreutoidea (Rota and Kristensen 2011), leaving its actual position uncertain. Recent molecular phylogenies have placed Millieriidae sister to Immidae (Regier et al. 2013) or in a clade with Urodidae and Schreckensteiniidae (Heikkilä et al. 2015), but with weak branch support in both analyses. Heppner (1982) implicitly stated that one of the three millieriid genera, *Phormoestes*, is diurnal, but diel activity for the other genera is unknown.

Tortricoidea and Pterophoroidea

Tortricoidea includes a single family, Tortricidae, which is mostly nocturnal. However, species with diurnally active adults are present in all three of the subfamilies defined by Regier et al. (2012a). Diurnal species can be found in the tortricine tribes Archipini, Ceracini, and Cochylini, and in the olethreutine tribe Grapholitini (Horak 1998; Monsalve et al. 2011; Kemal and Koçak 2014). Chlidanotinae, a primarily tropical subfamily, notably contains the brightly colored diurnal *Pseudatteria* (Roelofs and Brown 1982).

The Pterophoroidea, or plume moths, are predominantly nocturnal and are often observed flying early in the evening (Matthews 2008), though some species begin flying slightly earlier and would thus be considered both nocturnal and crepuscular (D. Matthews, personal communication). A few species in the Pterophorinae are diurnally active (e.g., *Geina tenuidactylus*) and have been seen feeding on nectar; many more species are also seen at flowers during the day, but only at rest (D. Matthews, personal communication).

Cossoidea, Sesioidea, and Zygaenoidea

The Cossoidea, Sesioidea, and Zygaenoidea form a monophyletic group and exhibit a wide range of diel flight patterns. The cossoid family Castniidae is exclusively diurnal; most species have colorful hindwings along with clubbed antennae, giving them a butterfly-like appearance (Miller 1986; Miller and Sourakov 2009). Brachodidae are largely diurnal although some species have been collected at night at lights (Kallies 2004; Kakul et al. 2006). Dudgeoneidae is composed of a single genus, *Dudgeonea*, that has been collected at lights and is suspected to be crepuscular (Common 1970). Similarly, the Metarbelidae have been collected at lights (Heppner 2008j). Cossidae, which does not constitute a monophyletic group in many recent molecular phylogenetic studies (Cho et al. 2011; Regier et al. 2009, 2013; Mutanen et al. 2010), is predominantly nocturnal. There are known exceptions in the genera *Dieida*, *Stygia*, and *Stygioides*, which have been seen flying during the day (Saldaitis et al. 2007; Yakovlev 2015).

Adults of Sesiidae (Sesioidea) and Himantopteridae (Zygaenoidea) are diurnal and exhibit remarkable wing morphology; sesiids have clear wings, giving them the appearance of wasps or bees (Laštůvka and Laštůvka 2001; Yagi et al. 2016), and himantopterids are brightly colored with long tails (Heppner 2008h). The evolution of sesiid wings is likely correlated with the shift to diurnality, since its involvement in both Batesian and Müllerian mimicry (Yagi et al. 2016) helps avoid bird predation, but it is unclear whether a similar correlation exists for Himantopteridae. In addition to Himantopteridae, Zygaenidae is the only other predominantly diurnal zygaenoid family. Zygaenids, like sesiids, often have wasp-like wing morphology and are part of mimicry complexes (Yen et al. 2005; Niehuis et al. 2006). Almost all adults of Aididae, Dalceridae, Lacturidae, and Megalopygidae are nocturnal (Sato et al. 1986; Epstein et al. 1998; Heppner 2008i; Zaspel et al. 2016). Limacodidae are also mainly nocturnal with the known exceptions of *Pantoctenia prasina*, which has been recorded mating during the day, and *Phobetron hipparchia*, a clear-winged mimic of Hymenoptera (Sato et al. 1986; Wagner 2005; Murphy et al. 2011). The Epipyropidae and Cyclotornidae are known for their similar, though unusual, life histories, where the larvae are parasitic on Hemiptera (Common 1990). However, whereas many epipyropid adults are active nocturnally (Epstein et al. 1998), cyclotornid adults are suspected to be crepuscular (Heppner 2008b).

Other non-obtectomeran moths

Relationships between the five remaining families of non-obtectomeran moths (Douglasiidae, Galacticidae, Immidae, Schreckensteiniidae, Urodidae) are unclear due to weak branch support in multiple studies (Regier et al. 2013; Heikkilä et al. 2015). However, there is variation in diel activity indicative of potential behavioral shifts. The diurnal Douglasiidae was traditionally considered a gracillarioid family, but recent molecular evidence places it within the Apodytrisia (Kawahara et al. 2011b). Immidae is believed to be entirely diurnal, though data is only available for a few species (e.g., species in *Birthana* (Braby 2015)). Schreckensteiniidae is also entirely diurnal (Heppner 2002). Urodidae contains crepuscular species that also exhibit diurnal (Landry 1998) or nocturnal (Frost 1972) behavior. For instance, *Wockia* (Landry 1998) is known to be diurnal and *Urodus* is nocturnal (Frost 1972). The Galacticidae, which were formally placed in the Urodidae, are presumed to be nocturnal (Heppner 2008d).

Papilionoidea

Papilionoidea is composed of the families Hedylidae, Hesperiidae, Lycaenidae, Nymphalidae, Papilionidae, Pieridae, and Riodinidae (Heikkilä et al. 2015). Nearly all papilionoids are considered diurnal, but our review of the literature yielded some ambiguities and exceptions to this generalization. In Nymphalidae, adult *Asterocampa celtis* have been observed dispersing to food sources at night (Langlois and Langlois 1964). A survey of diel activity in Brazilian Hesperiidae (Devries et al. 2008) revealed that the largest quantity of species are active in the late morning and early afternoon (900–1300). This survey was only conducted between sunrise and sunset, and consequently was inconclusive regarding crepuscular and nocturnal hesperiid activity. However, some hesperiids are often collected at lights at night (e.g., *Asora chromus* (Ormiston 1924), *Calpodes ethlius* (Kendall and Glick 1972), *Erionota*, *Gangara* (S. Maruyama, personal communication), and *Bungalotis* (Devries et al. 1987)). Although some reports of hesperiid nocturnality are likely anomalous cases in which a diurnal species happened to come to the light from a nearby bush, morphological variation implies that some reports are legitimate. Red eye coloration has been found more frequently in these nocturnal hesperiids, relative to diurnal species, indicating that red eyes may be correlated with nocturnal or crepuscular activity (Devries et al. 1987; Warren et al. 2009). Hedylidae are most frequently collected at night and are the sole primarily nocturnal family in Papilionoidea. They are also the only butterfly family that is known to have true tympanal organs (i.e., ears), which is thought to aid in bat-evasion during nocturnal flight (Yack and Fullard 2000). However, several hedylid species have been documented to fly during the day (Scoble 1990; Scoble and Aiello 1990), including *Macrosoma conifera* (Yack et al. 2007), one of the species used in our analysis. Without a comprehensive hedylid phylogeny, determining whether some hedylids have switched from an ancestrally nocturnal state to become secondarily diurnal remains unclear. Despite such exceptions, only minor ambiguity exists in our inferred evolutionary history of diel activity within Papilionoidea; the most recent common papilionoid ancestor was likely diurnal.

Thyridoidea and relatives

Thyridoidea, which contains the single family Thyrididae, is primarily nocturnal. There is one subfamily, Charideinae, whose species are apparently all diurnal, and are superficially very similar in appearance to the diurnal Zygaenidae (Dugdale et al. 1998). Diurnality has also been observed sporadically in the subfamily Thyridinae, such as in *Dysodia* and *Thyris* (Covell 2005).

The sister group to Thyridoidea is the Calliduloidea (Fig. S1), which contains diurnal, butterfly-like species (Yen et al. 2009). However, the Pterothysaninae contains at least one strictly nocturnal genus (the Afrotropical, monotypic *Caloschemia*) as well as the Southeast Asian *Pterothysanus*, which is both diurnal and nocturnal (Minet 1998). Griveaudiinae also contains species native to Madagascar that are nocturnal (Holloway 1998).

Thyridoidea + Calliduloidea is sister to a clade that contains the pterophorid genus *Agdistopis* and four superfamilies (Alucitoidea, Carposinoidea, Epermenioidea, Hyblaeoidea; Fig. S1). *Agdistopis* has been considered by some to be in its own family (Gielis and De Jong 1993) but not much is known about its diel activity. Similarly, little is known about the diel activity of Carposinoidea and Epermenioidea. One of the carposinoids included in the Regier et al. (2013) dataset, *Phycomorpha prasinochroa*, is nocturnal (Zborowski and Edwards 2007). Although Heppner (2008e) considers both families in this superfamily, Carposinidae and Copromorphidae, to be nocturnal, Davis (1969) reports a species that is both diurnal and nocturnal, so it is unclear whether nocturnality is truly present throughout the superfamily. Epermenioidea also appears to exhibit some variability in diel activity; multiple genera have been collected at lights at night and during the day via sweep netting (Dugdale 1987; Budashkin and Gaedike 2005). However, it remains unclear if the day-collected specimens were actively flying at the time of capture. Hyblaeidae, the only family within Hyblaeoidea, is believed to be nocturnal based on reported nocturnal behavior of one of the two genera in the family (*Hyblaea*, Sharma et al. 2013; N. Homziak, personal observation). Alucitoidea is generally considered to be nocturnal, with some observations of crepuscular activity (Pohl et al. 2015). Some species, such as *Alucita adriendenisi*, are known to fly during the day and night (Landry and Landry 2004).

Gelechioidea

Gelechioidea encompasses roughly 18,500 species (van Nieukerken et al. 2011) in some 16 families (Sohn et al. 2016). As the most taxonomically diverse superfamily of “micro-moths,” there is a dearth of behavioral data pertaining to individual species. There are a few predominantly diurnal lineages, namely Cosmopterigidae, Scythrididae, and Stathmopodidae (Willemstein 1987). The lack of behavioral data creates a challenge to infer diel activity across broader clades within the superfamily. However, we determined that the majority of sampled gelechioids in the Regier et al. tree were nocturnal, or likely nocturnal. We also note that it has been postulated that diurnal lineages exist within Autostichidae (specifically Deocloninae), Gelechiidae (Anacampsinae), Lecithoceridae, and Momphidae (Heppner 2008c).

Pyraloidea

The pyraloid families, Pyralidae and Crambidae, are mostly nocturnal (Beadle and Leckie 2012). Though there are individual examples of diurnal species, no clade, based on the current phylogeny of Pyraloidea (Regier et al. 2012b) appears to be entirely diurnal (J. Hayden, personal communication). Diurnal species have been recorded in the crambid subfamilies Glaphyriinae and Odontiinae (Wagner 1985; Gwynne and Edwards 1986). While nocturnal moths are known to produce ultrasound as an anti-bat defense (e.g., Blest 1964; Barber and Kawahara 2013; Kawahara and Barber 2015; Barber and Conner 2007; Fullard and Fenton 1977), it does not appear that ultrasound production in the Pyraloidea correlates to nocturnal activity. For example, the nocturnal greater wax moth, *Galleria mellonella* is known to produce ultrasound (Spangler 1985), but the diurnal odontiine *Syntonarcha iriastis* is also notable for having males that produce ultrasound for courtship purposes, using genital stridulation (Gwynne and Edwards 1986). Relatively few pyraloids are crepuscular, though some nocturnal species are also active at dusk, including the pest species *Plodia interpunctella* (Cowan and Gries 2009).

Drepanoidea and relatives

Drepanoidea has historically included several families, with conflicting classifications (e.g., van Nieukerken et al. 2011; Regier et al. 2013). While essentially all Drepanoidea are nocturnal, one drepanine tribe, Nedarini, has diurnal species restricted to Madagascar (Minet and Scoble 1998). The enigmatic family Doidae, which includes only six species in two genera, *Doa* and *Leuculodes*, has been placed in Drepanoidea (van Nieukerken et al. 2011), as recent molecular phylogenetic studies point to a close affinity with this superfamily (e.g., Regier et al. 2009, 2013; Mutanen et al. 2010; Bazinet et al. 2013). Doidae is generally considered to be at least partially diurnal (E. Braswell, personal communication). Brown (1990) notes that *Doa dora* has been observed displaying both diurnal and nocturnal behavior. *Leuculodes* have been collected at light and observed flying during the day (J. Adams, personal communication). Considering reports of diurnal and nocturnal behavior for both genera in Doidae, we cannot reasonably conclude as to whether the family is mostly diurnal or nocturnal. Clearly, additional behavioral work is warranted on this superfamily.

Two other superfamilies are closely related to Drepanoidea. Cimelioidea is a superfamily containing only six species, all of which are nocturnal (Minet 1998; Yen and Minet 2007). Mimallonoidea is currently believed to be the sister group to the Macroheterocera (e.g., Mutanen et al. 2010; Regier et al. 2013; Kawahara and Breinholt 2014), and nearly all species for which diel activity is known are nocturnal. Diurnality has only been observed in two mimallonid species, each in an apparently unrelated genus: *Cicinnus* and *Lacosoma*. These mimallonid species have darkly colored, sexually dimorphic diurnal males (St Laurent and Carvalho 2017).

Bombycoidea and Lasiocampoidea

Bombycoidea are perhaps some of the most well-studied moths due to their large size and charisma. Species in the Bombycoidea are primarily nocturnal, with only one taxon above the genus level (Saturniidae: Hemileucinae: Polythysanini) exhibiting diurnality in all species (but even so, only males are diurnal; all polythysanine females are nocturnal) (Lemaire 2002). Other instances of diurnal diel activity in Bombycoidea are more scattered, with only a handful of genera thought to be entirely or nearly entirely diurnal in at least one sex (e.g., Eupterotidae: *Hibrildes*; Bombycidae: *Rondotia*; Saturniidae: *Anisota*, *Callodirphia*, *Catharisa*, *Eochroa*, *Eupackardia*, *Heliconisa*, *Hemileuca*, *Ithomisa*, *Vegetia*). In cases such as *Anisota* and *Eupackardia*, diel activity varies between the sexes, with females diurnally active prior to and during copulation, nocturnal for oviposition, and males generally only displaying diurnal behavior (Tuskes et al. 1996; Lemaire 2002). Additionally, several species are reported to be diurnal within otherwise predominantly nocturnal genera, as well as a number of taxa where males are diurnal and females are not (e.g., Brahmaeidae: *Lemonia* (Lemaire and Minet 1998), Endromidae: *Endromis* (Heppner 2008f)). Sphingidae are a unique case because while several genera are strictly diurnal (e.g., *Hemaris*, some *Macroglossum*, most *Proserpinus*, *Sataspes*), crepuscular behavior is localized but found in a few genera (e.g., *Sphecodina*, *Sphingonaepiopsis*; I. Kitching, personal communication). Crepuscular genera are distantly related (Kawahara et al. 2009; Kawahara and Barber 2015), often with morphological adaptations unique to the crepuscular lineages (e.g., the very large eyes of the genus *Oryba,* I. Kitching (personal communication).

Lasiocampoidea, the sister group to the Bombycoidea, is a monotypic superfamily containing only the family Lasiocampidae (Regier et al. 2009; Zwick et al. 2011; Regier et al. 2013). Adults are nocturnal, though a number of exceptions exist where males fly during the day. For example, day-flying males have been documented in the Lasiocampinae (e.g., *Gloveria*, *Lasiocampa*, *Macrothylacia*), the Malacosominae (some Palearctic *Malacosoma*), and the Macromphaliinae (e.g., *Tolype*) (Franclemont 1973; Lemaire and Minet 1998; Jost et al. 2000; Fullard and Napoleone 2001; Powell and Opler 2009; Razafimanantsoa et al. 2012; Peigler, personal communication; Kawahara, Gough, St Laurent, personal observation; Zwick, personal communication).

Geometroidea

The geometroid families are generally nocturnal, except for the diurnal Epicopeiidae, which contains species notable for mimicking papilionid butterflies (Minet 2002). Its sister taxon, Pseudobistonidae, is nocturnal (Rajaei et al. 2015); therefore, epicopeiid diurnality is likely derived. Diurnality has also independently arisen in brightly colored, butterfly-like lineages of Uraniidae (Kite et al. 1991), a few species of Sematuridae (Minet and Scoble 1998), and in multiple clades of the geometrid subfamily Larentiinae (Ounap et al. 2016). A smattering of additional diurnal genera and species are known from other subfamilies of Geometridae; these groups tend to be brightly colored (e.g., *Dichromodes*, *Dysphania*, *Haematopis*, *Milionia*), or found at high latitudes (e.g., the boreal emerald moth *Mesothea incertata* (Ferguson 1985)). Crepuscular activity has been observed in a few Geometridae (e.g., *Alsophila* (Beadle and Leckie 2012)), and in some Sematuridae (Heppner 2008a). The monotypic sematurid subfamily Apoproginae, which had once been considered its own family, is strictly diurnal (Minet and Scoble 1998).

Noctuoidea

The vast majority of Noctuoidea are nocturnal, but three families (Notodontidae, Noctuidae, and Erebidae) include clades that are predominantly diurnal. The notodontid subfamily Dioptinae is almost exclusively diurnal, with only a handful of species that exhibit nocturnality (e.g., *Oricia hillmani*, *Xenomigia* spp. (Miller 2009)). Dioptine adults are often brightly colored, chemically defended, and part of numerous Neotropical mimicry complexes (Miller 2009). The Noctuidae includes two subfamilies where diurnal activity is widespread: the Heliothinae, which includes many colorful species that are active during the day (Hardwick 1996), and the Agaristinae, which includes a number of brightly colored diurnal species (Kitching and Rawlins 1998) that often have reduced eyes relative to the nocturnal agaristines (Poole 2014). In other noctuid subfamilies, such as the Noctuinae (Lafontaine 1987, 1998, 2004), Plusiinae (Lafontaine and Poole 1991), and Xyleninae (Mikkola et al. 2009), species occurring at high latitudes and altitudes tend to be diurnally active. Isolated examples of diurnality occur in other noctuid subfamilies, such as the stiriine *Xanthothrix* (Poole 1994), and the pantheine *Eucocytia* (Zahiri et al. 2013). Poole (1994) noted that diurnal noctuids possess reduced, ellipsoid eyes relative to nocturnal species in the family. In the Erebidae, diurnal activity is most common in the Arctiinae, many diurnal species of which mimic Hymenoptera (Weller et al. 2009), but some are also known to fly at night (Common 1990). The other erebid subfamilies are principally nocturnal, with a few exceptions, such as the diurnal or crepuscular Lymantriinae (Ferguson 1978), and a single erebine genus, *Cocytia*, which is a diurnal hymenopteran mimic (Kitching and Rawlins 1998).

Conclusions

Our study presents the first attempt at a synthesis of diel activity in Lepidoptera. We found and assembled diel activity data for 158 of the 483 species (32.7%) present in the Regier et al. (2013) phylogeny and discussed diel data for many more that we were able to uncover from the literature and other sources. Despite the absence of diel data for some lineages, our analysis inferred that diurnality is the likely ancestral condition in the order. Conversely, nocturnality was the dominant condition in the Ditrysia, which comprises ~98% of described lepidopteran species (van Nieukerken et al. 2011). Relatively few species were found to be truly crepuscular, and shifts toward this behavior appear to have occurred independently at least seven times (Fig. S1). Our analysis found limited instances of crepuscular taxa shifting from an ancestrally diurnal condition (in Hepialidae and Hesperiidae). There were 49 shifts from nocturnality to diurnality in our analysis (Fig. S1), though there are many more shifts that can be inferred from the literature, but are not present in the tree due to limited sampling (e.g., shifts in Carposinidae and Uraniidae). A few groups are predominantly diurnal (e.g., Castniidae, Epicopeiidae, and most butterfly families) and some are predominantly nocturnal (e.g., Bombycidae, Cossidae). However, most superfamilies and families had more than one state of diel activity represented, implying that many diel activity switches have occurred across the order. Based on the species richness counts of van Nieukerken et al. (2011), we estimate that roughly 75-85% of the described Lepidoptera species are nocturnal, 15-25% of Lepidoptera species are diurnal, and a small fraction of the total species diversity is truly crepuscular.

Several general trends can be concluded from this synopsis. First, species determined to be diurnal include many with colorful wings. The most prominent example is the butterflies, a group containing ~ 18,700 species (van Nieukerken et al. 2011) that are thought to be nearly entirely diurnal. Many of the brightly colored day-flying moths are known to be chemically defended or palatable mimics of toxic models, while others tended to visually resemble harmful Hymenoptera (e.g., ctenuchine erebids, Sesiidae, Zygaenidae, the thyridid subfamily Charideinae). Second, many diurnal species that are nested in nocturnal clades are found at high latitudes (e.g., the noctuid genera *Euxoa* and *Feltia*, the geometrid *Mesothea incertata*), high elevations (e.g., the saturniid genera *Callodirphia* and *Ithomisa*, the erebid genus *Gynaephora*), or are active in the autumn and winter (e.g., the saturniid genus *Hemileuca*). Some moths may have adapted to diurnality in these conditions to avoid flying in cooler air temperatures at night, which can cause an increased physiological burden (Comeau et al. 1976). It is also possible that diurnality at high latitudes may simply be a consequence of the increase in daylight hours, or a decrease in available predators. Third, a strong correlation appears to exist between diel activity and presence of acoustic sensory organs (i.e., ears). Butterflies, for example, are predominantly diurnal and lack ears (with a couple exceptions, such as *Hamadryas* (Yack 2004)), but the predominantly nocturnal Hedylidae have ultrasonic hearing organs (Yack et al. 1999; Minet and Surlykke 2003). Additionally, moths that are diurnal or live in habitats without predatory bats lack hearing organs or have less sensitive ones (Fullard et al. 1997; Muma and Fullard 2004). Therefore, the multiple origins of ears in nocturnal Lepidoptera (Scoble 1992; Ratcliffe and Fullard 2005; Barber and Kawahara 2013; Kawahara and Barber 2015) may have been an adaptation against insectivorous bats (Roeder and Treat 1970; Fullard 1982; Kristensen 2012). The evolution of diel activity was recently studied across mammals (Maor et al. 2017), but it remains largely unknown when specifically they are active during the night. Quantifying the activity times of bats is an important component in efforts to elucidate the mechanisms that structure moth diel activity patterns (Rydell et al. 1996).

Our phylogeny of diel activity in Lepidoptera can be used to explore multiple different avenues of future research. For example, this study can be used as a baseline to understand how diel activity influences the evolution of sensory organ morphology and of genes associated with dark and light environments. It has long been presumed that nocturnal insects developed eyes to see color (or UV patterns) at night (Kelber et al. 2003), and a species' shift between being active in a light or dark environment may drive sensory organ morphology and selection on relevant genes. Eye morphology appears to be fundamentally different in some diurnal taxa compared to their sister groups (Poole 1994), which also appears to be true at the intergeneric level (e.g., the large eyes of *Oryba* relative to other macroglossine hawkmoths). It would be interesting to construct a fossil-calibrated, dated tree to examine how vision has evolved in conjunction with day/night transitions across the phylogeny, which is the objective of one of our future studies.

We synthesized data on diel activity into three categories (day, night, crepuscular). However, it is well known that some Lepidoptera fly at specific times during these periods of the day (Fullard and Napoleone 2001; Lamarre et al. 2015). For instance, butterflies such as *Curetis bulis stigmata* fly in the late morning and early afternoon (between 1000 and 1300 at ~ 27° N (Singh 2014)), whereas the Neotropical *Heliconius sara* is generally only observed flying in the morning until 1130 (Rocha and Duarte 2001). Within Bombycoidea, the flight activity of Saturniidae often occurs late in the night (Janzen 1984), whereas some species of Sphingidae are only active early in the night, just after dusk (Beck and Linsenmair 2006; Lamarre et al. 2015). While there is a growing amount of literature on activity times for insects (e.g., Lamarre et al. 2015), knowledge gaps, especially for the micro-moths, remains substantial. Studies that have examined activity have predominantly relied on light trapping as a method for activity time assessment, which can be misleading as it may be biased to attract certain taxa, depending on the wavelength of light used (Merckx and Slade 2014). Light trapping also requires regularly sampling throughout the night, and many moths are known to land on vegetation near the light before flying to the collection area (Beck and Linsenmair 2006). An approach that does not rely on light to fully understand the activity times of nocturnal Lepidoptera is much needed.

Due to the large knowledge gaps in many lepidopteran lineages, additional behavioral data needs to be collected by taxonomists, ecologists, and naturalists. The advent of new social media platforms makes it easier for amateur naturalists to share their observations on butterflies and moths, and for scientists to assemble and assess the validity of these data. Such collaboration will greatly further our ability to truly understand the behavior of these charismatic insects.

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