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Movement and olfactory signals: Sexually dimorphic antennae and female flightlessness in moths

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Darwin argued a role for sexual selection in the evolution of male sensory structures, including insect antennae, the strength of which will depend upon the importance of early arrival at receptive females. There is remarkable variation in the nature and degree of sexual dimorphism in moth antennae, with males of some species having spectacular, feathery antennae. Although it is widely assumed that these elaborate structures provide greater sensitivity to chemical signals (sex pheromones), the factors underlying the interspecific diversity in male antennal structure and size are poorly understood. Because male antennal morphology may be affected by several female life–history traits, including flight ability, we conducted a phylogenetic comparative analysis to test how these traits are linked, using data from 93 species of moths across 11 superfamilies. Our results reveal that elaborate antennae in males have evolved more frequently in species where females are monandrous. Further, female loss of flight ability evolved more frequently in species where males have elaborate antennae. These results suggest that elaborate antennae have evolved in response to more intense male competition, arising from female monandry, and that the evolution of elaborate antennae in males has, in turn, shaped the evolution of female flightlessness.

KEYWORDS

sex pheromone, sexual selection, mating system, antennal morphology, flightless moth, mate location

Introduction

Signalling is a crucial component of reproduction for mobile diecious species, playing a role in both bringing mates together and in facilitating mechanisms of pre-mating sexual selection (e.g., Darwin, 1871; Andersson, 1994; Rosenthal, 2017). The latter is responsible for the evolution of an extraordinary diversity of conspicuous, sexually selected signals, across the range of sensory modalities, and has attracted very extensive research interest. In many moths, females use sex pheromones (olfactory

signals) to advertise their location to mate searching males. Although long-distance location-revealing sex pheromones are typically not regarded as being subject to sexual selection [see [Johansson and Jones \(2007\)](#)], they may cause sexual selection to act on male receptor organs ([Darwin, 1871](#); [Elgar et al., 2019](#)).

[Darwin \(1871\)](#) suggested that sexual selection will favour improvements in “organs of sense” if that improves the likelihood of male mating success in a competitive environment. Darwin did not explicitly mention antennae as “organs of sense,” because pheromones and the odour receptors located on antennal sensilla (e.g., [Hansson, 1995](#)) were not known at that time ([Elgar et al., 2019](#)). Nevertheless, his perspective suggests that selection will favour males with antennal features that improve the speed of detection of sex pheromones if that allows males to locate females more quickly than rival males. The taxonomically widespread sexual dimorphism in insect antennal morphology (e.g., [Schneider, 1964](#); [Elgar et al., 2018](#)), together with several lines of empirical evidence, are consistent with this perspective ([Elgar et al., 2019](#)). Field experiments on a sexually dimorphic moth, the gum-leaf skeletonizer *Uraba lugens*, demonstrated that males with longer antennae were more likely to detect lower amounts of pheromone ([Johnson et al., 2017b](#)), and laboratory experiments with the same species revealed that larvae developing in higher densities (thereby anticipating greater reproductive competition as adults) resulted in males with larger antennae and testes ([Johnson et al., 2017a](#)), and in females releasing more attractive sex pheromone ([Pham et al., 2020](#)).

Sexual dimorphism in some species of moths is remarkably striking, with the elaborate, feathery, pennate antennae of males contrasting with the simple threadlike or filiform antennae of females ([Schneider, 1964](#); [Young, 1997](#)). Phylogenetic comparative analyses indicate that while elaborate antennae are linked with larger body size, suggesting a functional cost to these structures, this pattern is not necessarily consistent with a greater capacity to detect chemical signals, because larger females might be expected to release larger quantities of pheromone ([Symonds et al., 2012](#)). On the other hand, in species where males have elaborate antennae, there is a negative correlation between male abundance and male antennal length. This result suggests that lower population densities with concomitantly lower concentrations of pheromone, may select for larger antennae in males, at least in species where males have elaborate antennae ([Symonds et al., 2012](#)). Regardless, males of most moth species possess relatively simple filiform antennae, whilst females still emit long-distance sex pheromones. This suggests that the strength of selection on male antennal morphology is linked to other factors that determine the importance of quickly locating a female, and thus rapidly detecting her sex pheromone. A previous comparative analysis of male elaborate antennae in geometrid moths ([Javoiš et al., 2019](#)) found that they were more likely to be found in species where females were capital breeders (i.e.,

that eclose with greater body reserves already available for breeding). [Javoiš et al. \(2019\)](#) suggested that such a strategy may be associated with traits that make them more difficult for males to locate quickly, such as reduced mobility.

There is emerging interest in the effects of movement on the production and detection of signals and cues, although research is largely confined to visual and auditory sensory modalities ([Tan and Elgar, 2021](#)). Nevertheless, movement may be consequential for chemical signalling: female moths may adjust the detectability of their sex pheromones by selecting different kinds of locations where they call (emit pheromones). For example, pheromones released in closed habitats may be less easily detected, and females may compensate by moving to a more open location ([Murlis et al., 1992](#)). Clearly this option is not available to less mobile, flightless female moths. Females are flightless in roughly 1% of lepidopteran species, although it is taxonomically widespread, occurring in 25 families ([Sattler, 1991](#)). Female wing loss in these species varies from a complete loss of wings (aptery) to retaining full sized wings but with a loss of function ([Tweedie, 1976](#); [Sattler, 1991](#)). Flightlessness is associated with winter-active adults and spring feeding, as well as high host breadth ([Hunter, 1995](#)). In most flightless species, the females are unable to move far and remain on or near their pupation site throughout their typically short adult life ([Sattler, 1991](#)). [Hackman \(1966\)](#) noted that these locations may not necessarily be optimal for calling and suggested that this selects for greater sensitivity to the pheromone in males. The converse may also be possible: that loss of flight evolved in part due to the speed with which highly sensitive males can locate females.

Here we use a phylogenetic comparative approach to examine several potential selection pressures favouring male antennal complexity in moths, including flightlessness and other life-history traits. Specifically, we ask whether certain female traits that potentially reduce their reproductive window (i.e., monandry, short lifespan, and the stage of egg development) are associated with the evolution of elaborate male antennae. Our hypothetical framework is that rapid location of a female would be favoured under female monandry, or when females eclose with a full complement of eggs (proovigeny): slower males may arrive after a female has mated and is no longer receptive, or after she has commenced ovipositing, and thus their sperm will fertilise fewer eggs ([Jervis et al., 2005](#); [Shuker, 2014](#)). We hypothesise that these female life-history traits would likely increase the level of competition among males and increase the strength of selection favouring elaborate antennae, because such antennae should increase the male's likelihood of locating the female more quickly.

Subsequently, we explore the links between male antennal morphology, female life-history and the evolution of female flightlessness. We specifically test the hypothesis proposed by [Hackman \(1966\)](#) that female flightlessness will be associated with the need for greater male sensitivity to sex pheromone, and hence with male elaborate antennae.

Materials and methods

Data collection

We collected information on female mating strategy, male antenna type, female flight ability, egg development, oviposition behaviour, lifespan, and fecundity for 93 species of moths from 11 superfamilies. The species were selected based on the availability of these data, which were collated from various sources including published literature, field guides and online lepidopterist resources (see [Table 1](#)).

We characterised male antennae as either simple or elaborate: the former is filiform or ciliate, whereas elaborate antennae have one or more side branches (pectinate, bipectinate, quadripectinate). Information on male antennae was obtained from published descriptions or images from various resources (see [Table 1](#) for a full list). Females were designated as capable of flying (macropterous) or flightless: flightless females may still have wings, but do not fly (e.g., *Lymantria dispar*) or may be brachypterous (small remnant wings) or apterous (wingless).

Mating strategies of females were classified as either monandrous or polyandrous, using information on female remating frequencies (mating frequency of males was not taken into account, as less information is available on this). Monandrous species are those with a remating frequency of 30% or less. This is a conservative value compared with rates previously used to categorise monandry [for example, <50% in [Arnqvist et al. \(2000\)](#), and <40% in [Torres-Vila et al. \(2002\)](#)]. Where detailed data on remating frequency were not available, we followed published qualitative descriptions of species as being either monandrous (including mostly monandrous) or polyandrous.

Females were classified as either synovigenic (continuing to form eggs during their adult life) or proovigenic (eclosing as an adult with a full complement of mature eggs). Species where females eclose with some mature eggs but produce more as an adult were classified as synovigenic. We also distinguished between females that oviposit eggs singly, in multiple small clutches of eggs, or in a single clutch. We then made this classification binary by combining the data for species in the latter two categories who did not lay eggs singly, as this was necessary for statistical analysis (see below). The fecundity and lifespan of the females were obtained from published papers, and we included the midpoint if a range was given. Fecundity was the total reported number of eggs laid over the lifespan. Female lifespan was the average number of days as an adult, as observed in natural field populations where possible. Finally, as body size may affect aspects of mating behaviour ([Blanckenhorn, 2000](#)) and male antennal morphology ([Symonds et al., 2012](#)), we also obtained measures of the maximum wingspan to use as a proxy for body size ([Miller, 1977, 1997](#)). We included male wingspan if the wingspan of both sexes were reported, and the midpoint of the range if a range was reported.

Phylogenetic comparative analysis

We used phylogenetic comparative methods to control for common ancestry ([Harvey and Pagel, 1991](#)) in our analysis of evolutionary associations between traits. There is no single phylogeny that incorporates all the species in our sample, and genetic data covering these species is sufficiently poor to make phylogenetic estimation unreliable. Following recommendations by [Beaulieu et al. \(2012\)](#), we compiled a composite phylogeny from the published phylogenies of the families included in our sample. The full tree, along with character mapping for binary traits, is presented in [Figure 1](#).

The main framework for the phylogeny was the superfamilial tree constructed by [Heikkilä et al. \(2015\)](#). The superfamilies Hepialoidea, Sesoidea, and Zygaenoidea each contained two species only, and so further resolution was not necessary. Any species from the same genus were also grouped together. We used the phylogeny from [Regier et al. \(2012b\)](#) to resolve relationships within the Pyraloidea. No further details were available for the Phycitinae family, leaving this group of eight species as a polytomy except for those species from the same genus, which were grouped together. The Tortricoidea were resolved to species level where possible following [Regier et al. \(2012a\)](#). Within the Tortricoidea, *Paralobesia viteana* was absent from all published phylogenies and therefore its position was left unresolved as a basal polytomy within this clade. The Archipini was also lacking detail on species from our analysis leaving those four species unresolved. [Sohn et al. \(2013\)](#) was used to fully resolve the Yponomeutoidea phylogeny, whereas [Löfstedt et al. \(1991\)](#) was used to resolve the three species in the genus *Yponomeuta*. The Bombycoidea phylogeny was taken from [Mutanen et al. \(2010\)](#). [Mutanen et al. \(2010\)](#) also provided further resolution to the Psychidae, although two species were missing rendering this group not fully resolved. [Yamamoto and Sota \(2007\)](#) and [Sihvonen et al. \(2011\)](#) were used to resolve the Geometroidea to subfamily, but no further details were available for all species present in our phylogeny leaving the six species of the Ennominae unresolved as well as the three species in the genus *Operophtera*. The Noctuidae were resolved using [Zahiri et al. \(2013\)](#), and the *Lymantria* phylogeny was taken from [Sutrisno \(2014\)](#). The superfamily Gracillariidae was fully resolved using the phylogeny from [Regier et al. \(2013\)](#). Relationships within the Gelechiidae were taken from [Kaila et al. \(2011\)](#) and [Heikkilä et al. \(2014\)](#).

In the absence of branch length information, all branches were assigned equal length (=1). The exception to this rule was cases where there remained uncertainty over the branching pattern; any polytomies were arbitrarily resolved but the resolved branches were assigned minimal branch lengths of 0.00001, giving them negligible weight in the analyses. This resolution was necessary because the phylogenetic comparative analysis approach requires fully dichotomously resolved phylogenies.

TABLE 1 Classification of species for traits examined.

Species	AS	FA	MS	ED	OB	LS	F	WS	References
<i>Acentria ephemerella</i>	S	F			B	1	180	12	3, 18, 28, 125
<i>Achroia grisella</i>	S	M	M			20		18.5	12, 27, 66, 107, 229
<i>Adoxophyes orana</i>	S	M	P		M		300	19.5	25, 156, 215, 222
<i>Alsophila pometaria</i>	S	F	M	P	B		100	27.5	37, 150, 171, 188
<i>Anarsia lineatella</i>	S	M			M	24	120	13.5	55, 87, 152, 194
<i>Auchmophila kordofensis</i>	E	F			B	21		30	133
<i>Austromusotima camptozonale</i>	S	M	M		M	5.7			24, 241
<i>Autographa gamma</i>	S	M			S	12	210	40	37, 85, 138, 230
<i>Biston betularia</i>	E	M		P	M		670	52.5	37, 106, 171
<i>Bupalus piniaria</i>	E	M			M	10	150	35	16, 44
<i>Cadra cautella</i>	S	M	P	S			200	17	12, 106, 124, 142, 143, 229
<i>Callimorpha (Panaxia) dominula</i>	S	M	M		S	6.25	250	48	50, 51, 71, 230
<i>Chilo suppressalis</i>	S	M	M			10	250	22	54, 108, 159, 160, 206
<i>Chloridea (Heliiothis) virescens</i>	S	M	P	S	M		800	32	140, 164, 175, 201, 211, 215, 229
<i>Choristoneura fumiferana</i>	S	M	P	S	M		94	22.5	57, 184, 215, 225, 229
<i>Choristoneura rosaceana</i>	S	M	P	S			750		29, 57, 136
<i>"Cnephasia" jactatana</i>	S	M	P	S			137		109, 110, 111, 161
<i>Corcyra cephalonica</i>	S	M	M	S	S	8.2	160	17	68, 163, 189
<i>Cornutiplusia circumflexa</i>	S	M							129, 138, 185
<i>Cryptoblabes gnidella</i>	S	M	M	S	M	12.7	105	15	9, 100, 151, 238
<i>Cydia pomonella</i>	S	M	P	P	S	17	200	18.5	26, 96, 120, 229
<i>Dahlica lichenella</i>		F	M		B	10	70	15	64
<i>Dasystoma salicella</i>	S	F			M	10	440	18.5	48, 112, 174
<i>Desmia funeralis</i>	S	M			S	9	200	25	19
<i>Diparopsis castanea</i>		M	P	S	S	11.4	152	30	45, 106, 137
<i>Earias insulana</i>	S	M	P	S		7	300	16.5	8, 115, 116, 201, 203, 229
<i>Elcysma westwoodi</i>	E	M	M		M				121, 122
<i>Ephestia elutella</i>	S	M	P		M	21	175	17	10, 124, 189
<i>Ephestia kuehniella</i>	S	M	P	S	S	9	264	2.25	7, 106, 114, 124, 189, 208, 239
<i>Epiphyas postvittana</i>	S	M	P	S	M		400	18.5	25, 72, 73, 82, 110, 126, 215
<i>Epirrita autumnata</i>	S	M	M	P	S	10	150	35	5, 89, 197, 205, 207
<i>Etiella hobsoni</i>	S	M	M				65		63, 157
<i>Etiella zinckenella</i>	S	M	M	S		10	166	25	63, 88, 135, 229
<i>Euproctis chrysorrhoea</i>	E	M			M		200	37.5	37, 74, 80, 118, 139
<i>Euxoa messoria</i>	E	M	M	S	S	14.2	1,303	34	29, 43, 65, 106
<i>Grapholita molesta</i>	S	M	P		S	34	245	12.5	11, 26, 33, 62, 96, 167
<i>Helicoverpa (Heliiothis) armigera</i>	S	M	P	S	S	9.75	380	35.5	52, 104, 158, 201, 229, 243
<i>Helicoverpa (Heliiothis) punctigera</i>	S	M	P	S	S		1,400		201, 243
<i>Helicoverpa zea</i>	S		P	S	S	15	600	38.5	2, 49, 69, 119, 201, 229
<i>Heterogynis penella</i>	E	F			B				123, 220
<i>Homoeosoma electellum</i>		M	M	S		14	337	19	58, 144, 183
<i>Hyalophora cecropia</i>	E	M	M	P				135	38, 182, 216, 229, 233
<i>Lambdina fiscellaria</i>	E	M	M		S	22.5	200		91, 92, 153, 197, 236
<i>Leucoma salicis</i>	E	M	P		M	9.4	650	45	75, 80, 221, 226, 229
<i>Leucoptera coffeella</i>	S	M	M	S	M	14	75	6.5	83, 132, 147, 148
<i>Lobesia botrana</i>	S	M	M	S	S		100	12	26, 100, 213, 215
<i>Lymantria dispar*</i>	E	F	M	P	B	8	800	50	34, 42, 80, 181, 226, 229

(Continued)

TABLE 1 (Continued)

Species	AS	FA	MS	ED	OB	LS	F	WS	References
<i>Lymantria fumida</i>	E	M							99, 226
<i>Lymantria mathura</i>	E	M			M		375	45	56, 226
<i>Lymantria monacha</i>	E	M	M	P	M		190	45	37, 80, 106, 192, 226
<i>Lymantria obfuscata</i>	E	F	M		M	7.6	285	31.8	60, 84, 209, 226
<i>Lymantria xyliana</i>	E	M			B		800		40, 195, 226
<i>Mamestra configurata</i>		M	P	S	M		2,150	40	97, 232
<i>Manduca sexta</i>	S	M		S	S		250	100	61, 117, 169, 229, 240
<i>Metisa plana</i>	E	F	M	P	B	7	155		177, 179
<i>Mnesampela privata</i>	S	M	M	S	M	11.8	300	41	196, 197, 201, 223, 224
<i>Mythimna separata</i>		M	P	S		6.5	850	35	94, 231
<i>Mythimna unipuncta</i>		M	P	S	M	14	1,500	40	32, 199
<i>Oiketicus kirbyi</i>	E	F	M		B		6,400		17, 177, 178
<i>Oncopera fasciculatus</i>	S	M	M		M		1,500		47, 131
<i>Operophtera bruceata</i>	S	F			S			27.5	75, 90, 170
<i>Operophtera brumata</i>	S	F	P	P	M	8.8	100	26.5	30, 90, 106, 218, 219, 229
<i>Operophtera fagata</i>	S	F						31.5	90, 193, 229
<i>Orgyia antiqua</i>	E	F	M	P	B	7	175	25	38, 106, 180, 204, 226
<i>Orgyia leucostigma</i>	E	F		P	B		167	32.5	38, 79, 204, 210
<i>Orgyia pseudotsugata</i>	E	F	M		B		180	34	67, 98, 200, 226
<i>Ostrinia nubilalis</i>	S	M	P	S	M	15	750	30	70, 106, 186, 229
<i>Paleacrita vernata</i>	E	F			M		251		29, 149, 171
<i>Panolis flammea</i>	S	M		S	M	11	100	36	106, 127, 128, 201
<i>Paralobesia viteana</i>	S	M			S	18.5	33	10	39, 100, 113
<i>Phigalia titea</i>	E	F			M		110	35	31, 53, 170, 171
<i>Phthorimaea operculella</i>	S	M	P	S	M	18.3	100	14	46, 134, 155, 229
<i>Platynota stultana</i>	S	M	M		M		307	12.5	22, 78, 81, 233, 234
<i>Plodia interpunctella</i>	S	M	P	S			80	15.5	7, 50, 76, 106, 124, 215, 229
<i>Plutella xylostella</i>	S	M	M	S	S	18.8	100	13	106, 202, 227, 229
<i>Siederia listerella</i>		F	M		B	10	50	15	64
<i>Sitotroga cerealella</i>		M	P		M	11.5	125	11.2	4, 189
<i>Sparganothis sulfureana</i>	S	M			M			20	59, 78, 168,
<i>Spodoptera exigua</i>	S	M	P	P	M	13.9	1,000	27.5	1, 37, 212, 214, 245
<i>Spodoptera littoralis</i>	S	M	P	S	M	16	1,800	38	6, 77, 115, 187, 229
<i>Spodoptera litura</i>	S		P	S	M		1,849	30	106, 141, 190, 245
<i>Sitthenopsis argenteomaculatus</i>	S	M						80	37
<i>Synanthedon pictipes</i>		M	M	S	S	9.2	140	24.5	106, 176, 237
<i>Teia anartoides</i>	E	F	M	P	B		400	25	41, 86, 198, Pers. Obs.
<i>Thyrocopa kikaelekea</i>	S	F							145
<i>Trichoplusia ni</i>	S	M	P	S	S	18	1,500	35.5	191, 228, 229, 242, 244, 245
<i>Utetheisa ornatrix</i>	S	M	P	S	M	17	350	37.5	23, 37, 101, 102, 103, 130
<i>Vitacea polistiformis</i>	E	M	M	P	S	7	350		21, 162, 166, 235
<i>Yponomeuta cagnagella</i>	S	M	P	S	M	50		23	13, 95, 146, 165, 217, 229
<i>Yponomeuta evonymella</i>	S	M			M	13			105, 146, 217
<i>Yponomeuta padella</i>	S	M	P		M	31			13, 93, 165, 173, 217

(Continued)

TABLE 1 (Continued)

Species	AS	FA	MS	ED	OB	LS	F	WS	References
<i>Zeiraphera canadensis</i>		M	M	S	M	28	79	13.5	35, 36, 154, 172
<i>Zeiraphera diniana</i>	S	M	M	S		30	150	19	14, 15, 20, 26

Male antennal structure (AS) = simple (S) or elaborate (E); Female flight ability (FA) = macropterous (M) or flightless (F); Female mating strategy (MS) = monandrous (M) or polyandrous (P); Egg development strategy (ED) = synovigenic (S) or proovigenic (P); Oviposition behaviour (OB) = single (S), multiple batches (M), or one batch (B); Lifespan of adult females (LS) = number of days; Fecundity (F) = number of eggs; Male wingspan (WS) = mm.

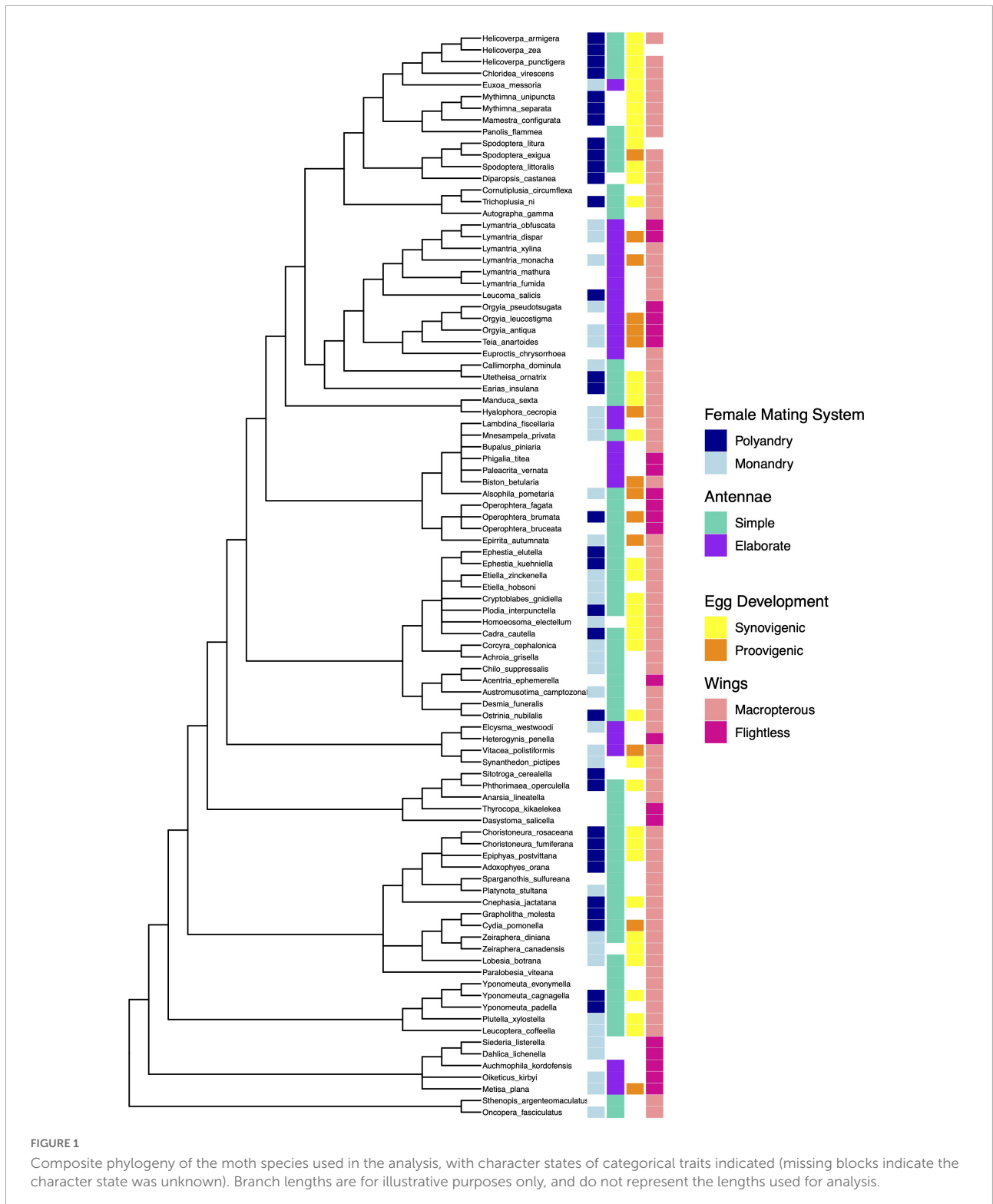
*The subspecies of *Lymantria dispar* used for this study was the European or North American spongy moth, which is flightless in nature and has the most available data.

¹Abdullah et al. (2000); ²Abernathy et al. (1994); ³Kipp et al. (2022); ⁴Akter et al. (2013); ⁵Ammunet et al. (2009); ⁶Anderson et al. (2007); ⁷Anderson and Lofqvist (1996); ⁸Anwar et al. (1973); ⁹Ascher et al. (1983); ¹⁰Ashworth (1993); ¹¹Atanassov and Shearer (2005); ¹²Australian moths online (2018) (moths.csiro.au); ¹³Bakker et al. (2008); ¹⁴Baltensweiler (1993); ¹⁵Baltensweiler and Fischlin (1988); ¹⁶Barbour (1988); ¹⁷Barnes (2002); ¹⁸Batra (1977); ¹⁹Bentley and Coviello (2012); ²⁰Benz (1969); ²¹Bergh (2012); ²²Bettiga (2013); ²³Bezzerides et al. (2008); ²⁴Boughton et al. (2007); ²⁵Bradley et al. (1973); ²⁶Bradley et al. (1979); ²⁷Brandt et al. (2005); ²⁸Buckingham and Ross (1981); ²⁹Bugguide (2017); ³⁰Buse and Good (1996); ³¹Butler (1985); ³²Capinera (2008); ³³Cardé and Baker (1984); ³⁴Cardé and Hagaman (1983); ³⁵Carroll (1994); ³⁶Carroll and Quiring (1993); ³⁷Carter (1984); ³⁸Carter (2004); ³⁹Cha et al. (2008); ⁴⁰Chao et al. (2001); ⁴¹Charles et al. (2006); ⁴²Charlton et al. (1993); ⁴³Cheng (1972); ⁴⁴Cheraghian (2013); ⁴⁵Chijikwa (2012); ⁴⁶Coll et al. (2000); ⁴⁷Common (1990); ⁴⁸Contant (1988); ⁴⁹Cook and Weinzler (2004); ⁵⁰Cook and Gage (1995); ⁵¹Cook and Wedell (1999); ⁵²Coombs et al. (1993); ⁵³Covell (2005); ⁵⁴Cuung and Cohen (2003); ⁵⁵Damos and Savopoulou-Soultani (2008); ⁵⁶European and Mediterranean Plant Protection Organization (2005); ⁵⁷Delisle et al. (2000); ⁵⁸DePew (1988); ⁵⁹Deutsch et al. (2015); ⁶⁰Dharmadhikari et al. (1985); ⁶¹Diamond et al. (2010); ⁶²Dustan (1964); ⁶³Edmonds et al. (2000); ⁶⁴Elzinga et al. (2011); ⁶⁵Encyclopedia of Life (2018) (eol.org); ⁶⁶Engqvist et al. (2014); ⁶⁷EPP0 (2017); ⁶⁸Etman et al. (1988); ⁶⁹Eviden et al. (2003); ⁷⁰Fadamiro and Baker (1999); ⁷¹Fisher and Ford (1947); ⁷²Foster and Ayers (1996); ⁷³Foster and Howard (1999); ⁷⁴Frago et al. (2009); ⁷⁵Furniss and Carolin (1977); ⁷⁶Gage (1995); ⁷⁷Gerling and Schwartz (1974); ⁷⁸Gilligan and Schwartz (2014); ⁷⁹Grant et al. (2014); ⁸⁰Grijpma et al. (1987); ⁸¹Groenen and Baixeras (2013); ⁸²Gu and Danthararajana (2000); ⁸³Guerreiro Filho (2006); ⁸⁴Gupta and Tara (2013); ⁸⁵Harakly (1975); ⁸⁶Harris (1988); ⁸⁷Hart (2006); ⁸⁸Hattori and Sato (1983); ⁸⁹Haukioja and Neuvonen (1985); ⁹⁰Hausmann and Viidalepp (2012); ⁹¹Hébert and Brodeur (2013); ⁹²Hébert et al. (2003); ⁹³Hendrikse (1986); ⁹⁴Hirai (1984); ⁹⁵Hora and Roessingh (1999); ⁹⁶Horak and Komai (2006); ⁹⁷Howlader and Gerber (1986); ⁹⁸Hunter (1995); ⁹⁹Identification guide of Japanese Moths (2018) (jpmoth.org); ¹⁰⁰Ioriatti et al. (2012); ¹⁰¹Iyengar and Eisner (1999); ¹⁰²Iyengar and Eisner (2002); ¹⁰³Iyengar et al. (2002); ¹⁰⁴Jallow et al. (1999); ¹⁰⁵Javois et al. (2005); ¹⁰⁶Jervis et al. (2005); ¹⁰⁷Jia and Greenfield (1997); ¹⁰⁸Jiao et al. (2006); ¹⁰⁹Jiménez-Pérez and Wang (2004a); ¹¹⁰Jiménez-Pérez and Wang (2004b); ¹¹¹Jiménez-Pérez et al. (2002); ¹¹²Jonko (2004–2022); ¹¹³Jordan, 2014; ¹¹⁴Karalius and Būda (1995); ¹¹⁵Kehat and Gordon (1975); ¹¹⁶Kehat and Gordon (1977); ¹¹⁷Keil (1989); ¹¹⁸Kelly et al. (1988); ¹¹⁹Kingan et al. (1993); ¹²⁰Knight (2007); ¹²¹Koshio (1996); ¹²²Koshio et al. (2007); ¹²³Kristensen (2003); ¹²⁴Landcare Research (2018). Manaaki Whenua (www.landcareresearch.co.nz); ¹²⁵Lau et al. (2007); ¹²⁶Lawrence and Bartell (1972); ¹²⁷Leather (1984); ¹²⁸Leather (1994); ¹²⁹Lepiforum e. V. (2018). (lepiforum.org) ¹³⁰Lim and Greenfield (2008); ¹³¹Madge (1954); ¹³²Magalhaes et al. (2008); ¹³³Mahmoud (2015); ¹³⁴Makee and Saour (2001); ¹³⁵Malinen (2007); ¹³⁶Marcotte et al. (2006); ¹³⁷Marks (1976); ¹³⁸Mazor and Dunkelblum (2005); ¹³⁹Mazzei et al. (1999–2022); ¹⁴⁰Mbata and Ramaswamy (1990); ¹⁴¹McCormack (2007); ¹⁴²McNamara et al. (2009a); ¹⁴³McNamara et al. (2009b); ¹⁴⁴McNeil and Delisle (1989); ¹⁴⁵Medeiros and Gillespie (2011); ¹⁴⁶Menken et al. (1992); ¹⁴⁷Michereff et al. (2007); ¹⁴⁸Michereff et al. (2004); ¹⁴⁹Miller et al. (1990); ¹⁵⁰Mitter and Klun (1987); ¹⁵¹Molet (2013); ¹⁵²Molinari and Zanrei (2004); ¹⁵³Moths of Canada (2016). Canadian Biodiversity Information Facility (2013–2017); ¹⁵⁴Mutuura and Freeman (1966); ¹⁵⁵Nabi and Harrison (1983); ¹⁵⁶Nagata et al. (1972); ¹⁵⁷Naito et al. (1986); ¹⁵⁸Naseri et al. (2009); ¹⁵⁹Moth Photographers Group (2020); ¹⁶⁰Nozato (1982); ¹⁶¹Ochieng-Odero (1992); ¹⁶²Olien et al. (1993); ¹⁶³Olsen (1995); ¹⁶⁴Park et al. (1998); ¹⁶⁵Parker et al. (2013); ¹⁶⁶Pearson et al. (2004); ¹⁶⁷Phillips and Proctor (1969); ¹⁶⁸Polavarapu et al. (2001); ¹⁶⁹Potter et al. (2011); ¹⁷⁰Powell and Opler (2009); ¹⁷¹Price (1997); ¹⁷²Quiring (1994); ¹⁷³Rajimann and Menken (2000); ¹⁷⁴Raine (1966); ¹⁷⁵Ramaswamy (1990); ¹⁷⁶Reed et al. (1988); ¹⁷⁷Rhainds and Gries (1998); ¹⁷⁸Rhainds et al. (1995); ¹⁷⁹Rhainds et al. (1999); ¹⁸⁰Richards et al. (1999); ¹⁸¹Richerson et al. (1976); ¹⁸²Riddiford and Ashenbush (1973); ¹⁸³Riemann (1986); ¹⁸⁴Robison et al. (1998); ¹⁸⁵Ronkay and Behounek (2015); ¹⁸⁶Royer and McNeil (1993); ¹⁸⁷Sadek (2001); ¹⁸⁸Schneider (1980); ¹⁸⁹Sedlacek et al. (1995); ¹⁹⁰Seth and Sharma (2002); ¹⁹¹Shorey et al. (1962); ¹⁹²Skuhavy (1987); ¹⁹³Snäll et al. (2007); ¹⁹⁴Sorenson and Gunnell (1955); ¹⁹⁵St. Laurent and McCarthy (2016); ¹⁹⁶Steinbauer (2005); ¹⁹⁷Steinbauer et al. (2001); ¹⁹⁸Suckling et al. (2007); ¹⁹⁹Svard and McNeil (1994); ²⁰⁰Swaby et al. (1987); ²⁰¹Symonds et al. (2012); ²⁰²Talekar and Shelton (1993); ²⁰³Tamhankar (1995); ²⁰⁴Tammaru et al. (2002); ²⁰⁵Tammaru et al. (1996); ²⁰⁶Tang et al. (2014); ²⁰⁷Tanhuanpää et al. (2003); ²⁰⁸Tarlack et al. (2015); ²⁰⁹Thakur et al. (2016); ²¹⁰Thurston and MacGregor (2003); ²¹¹Tingle and Mitchell (1991); ²¹²Tisdale and Sappington (2001); ²¹³Torres-Vila et al. (2002); ²¹⁴Torres-Vila et al. (2001); ²¹⁵Torres-Vila et al. (2004); ²¹⁶Tuskes et al. (1996); ²¹⁷Van der Pers et al. (1980); ²¹⁸Van Dongen et al. (1998); ²¹⁹Van Dongen et al. (1999); ²²⁰Vegliante (2005); ²²¹Wagner and Leonard (1979); ²²²Walker (2005); ²²³Walker and Allen (2010); ²²⁴Walker and Allen (2011); ²²⁵Wallace et al. (2004); ²²⁶Wallner (1989); ²²⁷Wang et al. (2005); ²²⁸Ward and Landolt (1995); ²²⁹Watson et al. (1975); ²³⁰Watson and Dallwitz (2003–2022); ²³¹Watson and Hill (1985); ²³²WCCP (1995); ²³³Webster and Cardé (1984); ²³⁴Webster and Cardé (1982); ²³⁵Weihman (2005); ²³⁶West and Bowers (1994); ²³⁷Wong et al. (1969); ²³⁸Wysoki et al. (1993); ²³⁹Xu et al. (2008); ²⁴⁰Yamamoto and Sota (2007); ²⁴¹Yen et al. (2004); ²⁴²Zacharuk (1985); ²⁴³Zalucki et al. (1986); ²⁴⁴Zhu et al. (1997); ²⁴⁵Ziaee (2012).

Following Ives and Garland (2014), we ran multiple tests to improve the strength of our inferences. These tests included generalised linear mixed models with Bayesian estimation (MCMCglmm) (Hadfield and Nakagawa, 2010) and the concentrated changes test (Maddison, 1990). The MCMCglmm models were conducted using the MCMCglmm package in R (Hadfield, 2010; R Core Team, 2014). To determine which traits are linked to our dependent variables when controlling for phylogenetic relatedness, all independent variables of interest were tested using MCMCglmm in separate models where wingspan was included as the covariate to control for body size. Specifically we performed one set of tests with antennal morphology as the dependent variable, coded as simple (1) and elaborate (2) antennae. In these tests the independent variables were female mating system (monandrous/polyandrous), egg development (proovigenic/synovigenic), and lifespan. In the second set of tests the dependent variable was female wing type coded as macropterous (1) or flightless (2). In these tests the

independent predictors were female mating system, lifespan, antenna type, egg development, oviposition strategy (single eggs laid/multiple eggs clutches), and fecundity.

These models cannot incorporate missing data; therefore, the data sets were reduced to include only those species where all data were available for the variables being tested in each analysis. These tests require a prior to be set, and when the response variable is categorical in nature the prior for the residual variance should be fixed. For our analyses, we set the residual variance to 1 and used a χ^2 distribution with 1 degree of freedom ($v = 1$, $nu = 1000$, $alpha.mu = 0$, $alpha.V = 1$) for the random effects variance, as suggested by Villemereuil et al. (2013). We used the categorical family response, and used the slice function to improve mixing. To obtain adequate mixing with low autocorrelation, 5×10^7 iterations were used with a 10,000 burnin period, followed by sampling every 2,500 iterations (thinning). The R code used in this procedure is provided in the Supplementary material.



The Concentrate Changes Test (CCT) was used to investigate the co-evolution of two binary discrete characters across a phylogeny, using the computer program MacClade 4 (Maddison and Maddison, 2005). CCTs examine changes

from one state to another in a character of interest (the dependent variable) and whether these are more concentrated in lineages that have evolved a particular state of interest in another character (the independent variable) than would be

expected by chance (determined by comparison with 1,000 permutations of the dependent variable on the phylogeny). When characters are mapped onto the phylogeny, the most parsimonious reconstruction of the character is applied for all species, including those with missing data, allowing us to leave all 93 species in each analysis. CCTs require a fully resolved phylogeny and we used MacClade to randomly resolve any polytomies 20 times in our composite phylogeny, performing the analysis on each tree individually, thereby yielding a mean p -value \pm SEM. For each pair of traits, the tests were run in both directions, with the independent and dependent traits switched, to determine the order of evolution. We also applied the test only to changes where the parsimonious resolution of the evolution of the dependent was unequivocal. These tests lack the statistical power of MCMCglmm, and cannot control for body size, but unlike the MCMCglmm, they do provide information about the direction of evolution (i.e., which correlated trait preceded the evolution of the other), and possible patterns of causality.

Results

We found a significant association between antennal type and female mating system (MCMCglmm analysis: **Table 2**), with the concentrated changes test indicating weakly ($p = 0.062$) that elaborate male antennae evolve more frequently in species where females are monandrous (CCT analysis: **Table 3**). Indeed, most species in our analysis with elaborate male antennae have monandrous females, whereas most species with simple male antennae have polyandrous females (**Figure 2A**). Similarly, male antenna type is also associated with egg development pattern, with elaborate male antennae being associated with proovigenic females (**Table 2**). Indeed, within our sample of species with elaborate male antennae, only one is synovigenic, producing eggs as an adult (**Figure 2B**). However, the CCT analysis suggests (again weakly: $p = 0.081$) that proovigeny has evolved more frequently in species where males have elaborate antennae (**Table 3**). The type of male antennae was not associated with female lifespan (**Table 2**).

We found a link between female flight ability and male antenna type (**Table 2**), with the CCT analysis suggesting that female flightlessness is more likely to have evolved in species where males have elaborate antennae, rather than *vice versa* (**Table 3** and **Figure 3C**). Female flightlessness is also associated with a shorter female lifespan (**Table 2**), and the association between flight ability and oviposition strategy (single eggs vs. batches) approached significance in the MCMCglmm analysis ($p = 0.056$, **Table 2** and **Figure 3D**). The CCT results suggest that flightlessness has evolved more often in species where females lay eggs in clutches (**Table 3**). While all the flightless species in our sample are proovigenic (**Figure 3B**), the lack of transitions from synovigenic to proovigenic severely limits the power for the MCMCglmm analysis, and these analyses did

not converge, so we do not include these tests in our analysis. Although most flightless species have monoandrous females (**Figure 3A**), the phylogenetic comparative analyses found no significant association between female flight ability and mating system, or between flight ability and fecundity (**Tables 2, 3**).

Discussion

Prevailing wisdom states that elaborate antennae in males evolved to increase their ability to detect odours (specifically the sex pheromone of females). However, this hypothesis is contradicted by the considerable number of moth species where males do not possess elaborate antennae, despite most species utilising long-distance female sex pheromones. Our results suggest a more nuanced version of the hypothesis where ability to detect and locate females quickly is advantageous in some species: elaborate male antennae being more common in species where females are monandrous, proovigenic, or flightless. Concentrated changes tests indicate that it is more likely that the evolution of elaborate male antennae is concentrated lineages where females are monoandrous rather than *vice versa* (suggesting that the mating system evolved prior to the antennal morphology). Similarly, that the CCTs suggest that female flightlessness is more likely to have evolved in lineages where elaborate male antennae had already evolved rather than the opposite, which argues against the **Hackman (1966)** hypothesis that female flightlessness selects for males with more sensitive antennae. These trends provide some insights into the conditions leading to the evolution of both male elaborate antennae and female flightlessness, and more generally highlight how olfactory signal perception can be linked with movement.

Darwin's (1871) conjecture that sexual selection favours male sensory receptor traits that improve the ability to detect and locate females more quickly is supported by the strong association between complex male antennal structure and female monandry. Female monandry places a premium on males being able to rapidly locate virgin females, whose numbers may decline during the male's adult lifespan, and larger or more elaborate male antennae apparently facilitate this process [see also **Johnson et al. (2017b)**]. This interpretation implicitly assumes that elaborate antennae bestow greater sensory capabilities, and this has been widely assumed in previous analyses of antennal morphology in moths (**Symonds et al., 2012; Javoš et al., 2019**). However, while elaborate antennae might facilitate the trapping of air flow and hence chemical compounds (**Loudon and Koehl, 2000**), the direct evidence that they have higher sensitivity is surprisingly rare. In this context exceptions to the patterns outlined above can be informative. For example, selection may still favour elaborate male antennae in the polyandrous satin moth *Leucoma salicis* because females initially oviposit a large clutch of eggs, and subsequently lay smaller clutches (**Wagner and Leonard, 1979**),

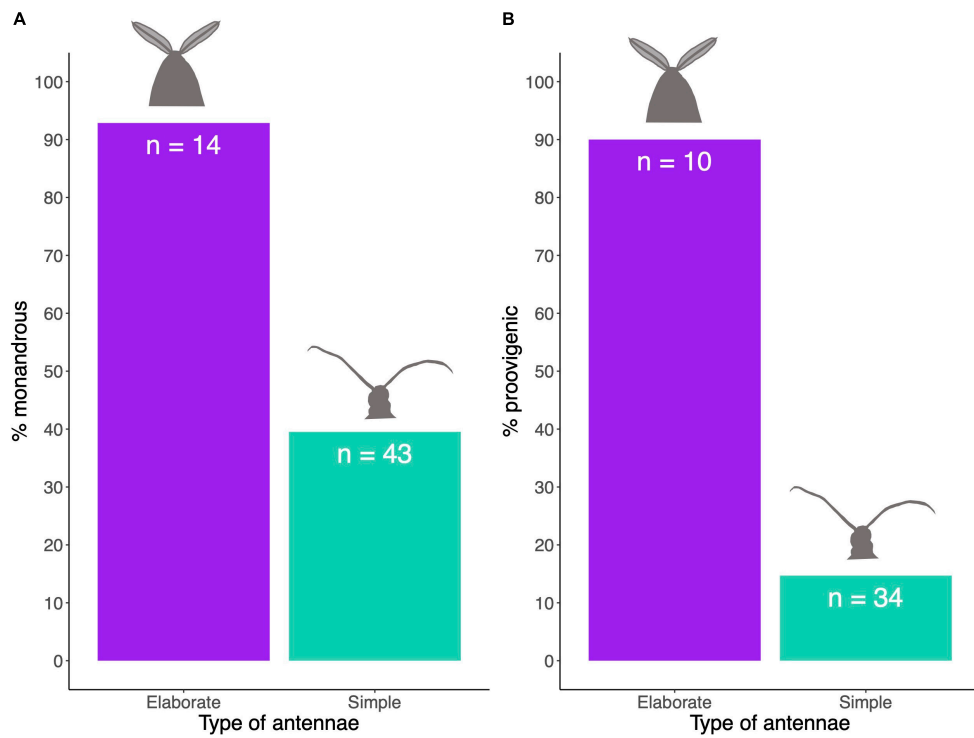


FIGURE 2 (A,B) Percentage of species with particular traits relative to the type of male antennae.

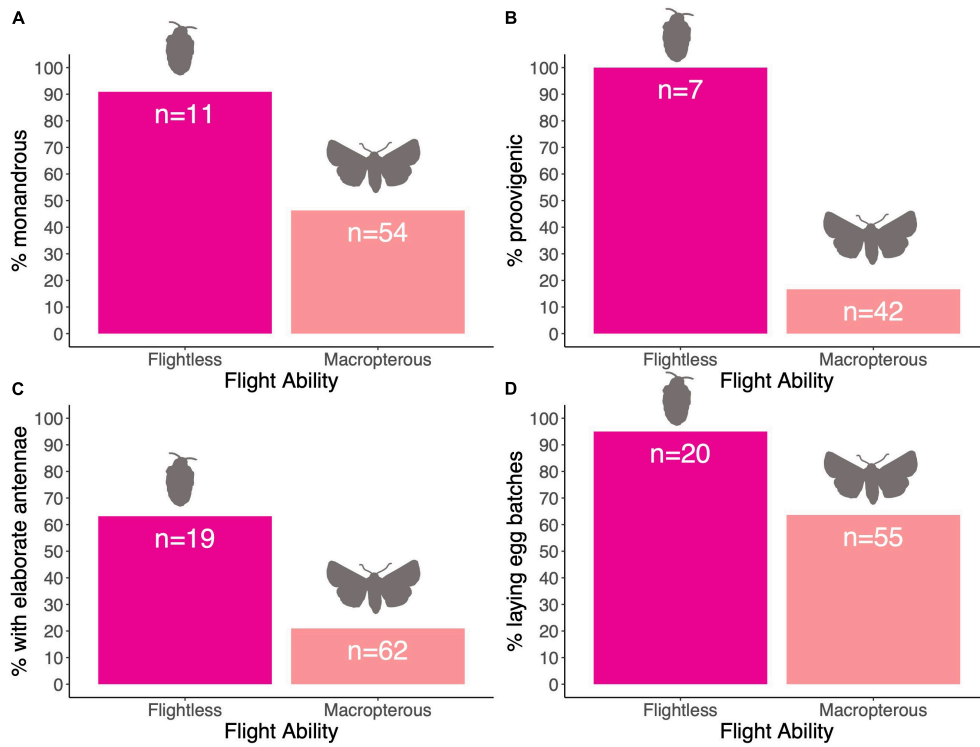


FIGURE 3 (A–D) Percentage of species with particular traits relative to the flight ability of female.

TABLE 2 Results from the MCMCglmm analysis comparing the dependent variable (male antennal type, female wing type) to the independent variable, controlling for body size (male wingspan).

Dependent variable	Independent variable	N		Posterior mean	95% CI	P-value
Male antennae—Simple (1), Elaborate (2)	Female mating system—Monandry (1), Polyandry (2)	45	Mating	-6.17	-13.69, 0.43	0.043
			WSpan	0.22	-0.01, 0.50	0.017
	Egg development—Synovigenic (1), Proovigenic (2)	39	EggDevel	7.59	1.02, 15.57	0.005
			WSpan	0.10	-0.02, 0.24	0.051
Female wing type—Macropterous (1), Flightless (2)	Female mating system—Monandry (1), Polyandry (2)	53	Lifespan	-0.15	-0.53, 0.20	0.410
			WSpan	0.16	-0.05, 0.39	0.112
	Female lifespan	48	Lifespan	-0.64	-1.29, -0.06	0.005
			WSpan	-0.002	-0.23, 0.23	0.979
	Male antennae—Simple (1), Elaborate (2)	62	Antennae	5.21	0.02, 10.92	0.028
			WSpan	-0.20	-0.43, -0.01	0.014
Oviposition—Single eggs (1), Egg batches (2)	60	Oviposition	4.47	-0.47, 10.3	0.056	
		WSpan	-0.17	-0.40, 0.04	0.08	
Fecundity	64	Fecundity	-0.002	-0.01, 0.01	0.556	
		WSpan	-0.16	-0.39, 0.04	0.113	

Each categorical variable was given a value (1 or 2) according to the state (e.g., polyandry = 2 and monandry = 1). N values for each model are listed. The model of wing type vs. egg development is not included due to lack of transitions with which to adequately test the relationship. Bold values indicate statistically significant relationships.

TABLE 3 Results from the concentrated changes test investigating evolutionary associations between discrete characters with the state of interest listed.

Character 1	Character 2	p-value ± SE (Character 1 = dependent)	p-value ± SE (Character 2 = dependent)
Male antennae—Elaborate	Female mating system—Monandry	0.062 ± 0.004	0.317 ± 0.008
	Egg development—Proovigenic	0.159 ± 0.011	0.081 ± 0.002
Female wing type—Macropterous	Female mating system—Monandry	0.093 ± 0.004	0.957 ± 0.002
	Male antennae—Elaborate	0.052 ± 0.003	0.676 ± 0.027
	Oviposition—Egg batches	0.076 ± 0.005	0.983 ± 0.001

Results are presented where characters are assigned as dependent or independent, and then *vice versa*. The p-value ± SE corresponds to the mean p-value obtained from the analysis of the 20 randomly resolved trees. N = 93 in all tests.

which places a premium on males locating virgin females. In this context, it is interesting that there is a relationship between egg development strategy and male antennal morphology, with proovigeny (where females eclose with their full complement of eggs) being associated with elaborate male antennae.

Although the large majority (>90%) of species with elaborate male antennae have monandrous females, males have filiform antennae in 17 of the 30 monandrous species in our sample. In these species, perhaps males with filiform antennae utilise other means of improving sensitivity in detecting female pheromones. For example, detectability may be improved by increasing the number and/or density of sensilla, changing the distribution of the sensilla (Keil, 1989; Lee and Strausfeld, 1990), or adjusting the angle of antennal scales (Wang et al., 2018). Additionally, features of the adult population, such as high population density (Symonds et al., 2012) or male flight speed, may relax selection on rapid detection. Finally,

male mating system may also affect the evolution of antennal morphology, although the nature of the relationship between typical male mating frequency and the strength of selection for greater detection capacity seems unlikely to be independent of other factors, including female mating strategy. Consequently it may be that it is overall mating strategy (monogamy vs. polygamy) that is the stronger determinant of selection on male antennal morphology.

Female flightlessness is thought to allow females to invest more resources in egg production, thereby yielding higher fecundity (Tweedie, 1976; Roff, 1990; Sattler, 1991). Our analyses revealed that female flightlessness is associated with a shorter adult lifespan and confining oviposition to a single clutch of eggs, an unsurprising pattern because laying eggs singly or across multiple clutches would require an ability to disperse to different oviposition sites (Sattler, 1991). However, there was no significant correlation between female

flightlessness and fecundity after controlling for phylogeny and body size. Hunter (1995) reported a positive correlation between female flightlessness and fecundity, but this pattern was phylogenetically constrained, and the correlation was no longer significant after taking account of phylogeny. Our analysis supports that finding. Nevertheless, we cannot rule out the possibility that females can improve reproductive success by increasing egg size rather than egg number. Indeed, the flight ability of female tussock moth *Orgyia thyellina* varies seasonally: individuals eclosing in autumn have reduced wings whilst those emerging in summer have fully functional wings (Kimura and Masaki, 1977). The flightless females produce much larger eggs than females that emerge in summer, a strategy that may improve the survival of eggs that diapause over winter. Males of *O. thyellina* have elaborate, bipectinate antennae (Table 1), and it would be interesting to know if there is a similar seasonal pattern in antennal size.

While our data broadly support the idea that the presence of elaborate antennae in males favoured the evolution of female flightlessness, there are seven species within our data set where females are flightless, and yet males have simple, filiform antennae (Figure 3). Interestingly, females in five of these species are still mobile, either by walking or hopping (Contant, 1988; Sattler, 1991; Medeiros and Gillespie, 2011), and females of the other two species have unusual biological features. Females of *Acentria ephemerella* are aquatic and the loss of flight is likely to be an adaptation that supports this lifestyle (Miler, 2008), highlighting that the evolution of female flightlessness is not linked exclusively with issues associated with mate search. The second species indicates that the strength of selection through mate search can override the relationship between elaborate antennae and flightlessness: around 80% of *Alsophila pometaria* females are pseudogamous asexuals (Mitter and Klun, 1987), who produce asexual offspring after mating, resulting in a strongly female-biased population. So, while the loss of flight has likely evolved due to similar pressures affecting other species in our data set, the pseudogamous nature of this species may relax selection favouring elaborate male antennae.

To conclude, our findings suggest that the communication and mating systems of moths are inherently associated, with elaborate male antennae being associated with lineages where females are monandrous, suggesting that necessity to detect females quickly has selected for more sensitive males. In turn male elaborate antennae may have subsequently driven the evolution of female life-history and flightlessness where having sensitive males promoted selection for complete development of eggs at the expense of movement capability. A key aspect of this narrative is that elaborate antennae in males is associated with greater sensitivity, an assumption that still needs to be more thoroughly tested in moths.

Data availability statement

The original contributions presented in this study are included in the article/Supplementary material, further inquiries can be directed to the corresponding authors.

Author contributions

TJ assembled the comparative data set. TJ and MS conducted the comparative statistical analyses. All authors conceived and designed the research, interpreted the data, prepared and edited the manuscript, and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2022.919093/full#supplementary-material>

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