

Biogeography and the evolution of flightlessness in a radiation of Hawaiian moths (*Xyloryctidae*: *Thyrocopa*)

Matthew J. Medeiros^{1*} and Rosemary G. Gillespie²

¹Department of Integrative Biology, University of California, Berkeley, CA 94720, USA,

²Department of Environmental Biology, University of California, Berkeley, CA 94720, USA

ABSTRACT

Aim Although the ability to fly confers benefits to most insects, some taxa have become secondarily flightless. Insect flightlessness may be more likely to evolve in environments such as islands and other windswept and alpine areas, but this prediction has rarely been tested while controlling for phylogenetic effects. Here we present a phylogeny for the endemic Hawaiian Lepidoptera genus *Thyrocopa*, which has two flightless species that occur in alpine areas on Maui and Hawaii islands, in order to determine whether the flightless species are sister to each other or represent separate losses of flight. We also explore divergence times and biogeographic patterns of inter-island colonization in *Thyrocopa*, and present the first Hawaiian study to sample a genus from nine islands.

Location The Hawaiian Islands.

Methods The phylogeny is composed of 70 individuals (including 23 *Thyrocopa* species and 7 outgroup species) sequenced for portions of cytochrome *c* oxidase subunit I, elongation factor 1 α and *wingless* genes, for a total of 1964 base pairs, and was estimated using both parsimony (PAUP*) and Bayesian inference (MRBAYES). Divergence times were estimated using the BEAST software package.

Results Our results indicate that two independent invasions of alpine habitats with concomitant loss of flight have occurred in *Thyrocopa*. Based on current taxon sampling, *Thyrocopa* colonized the Hawaiian Islands slightly before the formation of Kauai. In terms of overall patterns of diversification, subclades generally follow a progression from older to younger islands. The genus has the greatest number of species on Kauai, with species numbers generally decreasing with decreasing island age.

Main conclusions Loss of flight ability has evolved twice in a short period of geological time in *Thyrocopa*, perhaps as a result of low temperatures, high winds and/or a lack of predation pressure. However, several other *Thyrocopa* species that live on small islands with consistently high winds, such as Necker and Nihoa islands, retain the ability to fly.

Keywords

Dispersal, flightless insects, Gelechioidea, island evolution, Kahoolawe, Necker, Nihoa, Northwestern Hawaiian Islands, phylogeny.

*Correspondence: Matthew J. Medeiros, The Smithsonian Institution, Department of Entomology, Washington, DC, 20013, USA. E-mail: matt.j.medeiros@gmail.com

INTRODUCTION

The ability to fly confers numerous advantages to insects, but comes with a high energetic cost. Therefore, much debate has focused on determining the ecological conditions that favour secondary flightlessness in insects (Roff, 1990; Wagner & Liebherr, 1992; Dudley, 2000; Snäll *et al.*, 2007). For example,

homogenous and persistent environments (e.g. 'permanent woodlands') are purportedly correlated with a high incidence of flightlessness (Roff, 1990; Hunter, 1995; Snäll *et al.*, 2007; Wahlberg *et al.*, 2010), suggesting that in these habitats the ability to disperse, possibly to find food sources or oviposit, is not critical. Other habitats, such as alpine areas and caves, are also correlated with a higher than expected incidence of

flightlessness (Roff, 1990; Tauber *et al.*, 2007). Why this may be so is not entirely clear, but low temperatures and high winds are candidate correlates in alpine areas, while lack of resources and/or predators are likely explanations in caves. Coastal dune habitats are also associated with flightlessness, as in the case of the Californian moth *Areniscythris brachypteris* Powell, perhaps because winds are high and/or predation pressure is low (Powell, 1976). Despite the small body of published evidence to the contrary (Roff, 1990; Short & Liebherr, 2007), high winds and island or island-like habitats remain the leading ecological contexts of insect flightlessness. Authors ranging from Darwin (1859) to Sattler (1991) suggest that islands and/or high winds may be the most ubiquitous explanation for brachyptery (wing reduction), especially when it characterizes both sexes, because high winds could cause flying insects to stray off-course and become stranded in inhospitable areas, and because in some cases high winds impede pheromonal attraction, rendering male flight unnecessary (Sattler & Wojtusiak, 2000).

At least among many taxa that are passively dispersed by wind, if dispersal (flight) ability were not reduced there would be a high chance of individuals being transported off the island and lost at sea; within an island, individuals could be transported beyond the bounds of the narrow, stable habitats to which insular organisms often become adapted. This tendency appears to have played a major role in subsequent adaptive radiation [Carlquist, 1966, 1974, 1980; but see Roff's (1990) suggestion that the correlation between insular habitats and flightlessness may sometimes be spurious]. In order to ascertain whether high winds, habitat persistence, or any other ecological conditions generally lead to insect flightlessness, additional phylogenetic studies of insect groups exhibiting flightlessness (Wagner & Liebherr, 1992) are required, particularly for cases where we know that flightlessness evolved *in situ* and that the taxa in question were originally highly capable dispersers. Unfortunately, most assessments of the relationship between flightlessness (low dispersal capability) and habitat parameters have failed to control for the possible non-independence of phylogenetic effects (Roff, 1994), although there are some notable exceptions (e.g. Denno *et al.*, 1996; Wahlberg *et al.*, 2010).

The Hawaiian Islands provide an ideal location for studying the evolution of flightlessness on islands, particularly because their distance from any other landmasses is great enough that any taxon that successfully colonized them must have done so through active or passive long-distance dispersal. Diverse flightless insect taxa have evolved from flighted ancestors within the islands, including lineages in Orthoptera, Thysanoptera, Hemiptera, Neuroptera, Coleoptera, Hymenoptera and Diptera, as well as Lepidoptera (Perkins, 1913; Zimmerman, 1947; Ashlock & Gagné, 1983; Tauber *et al.*, 2007). However, brachyptery is not always a prerequisite for flightlessness: some cave-dwelling *Schrankia* (Lepidoptera: Noctuidae) individuals are flightless although their wings are not significantly reduced (Medeiros *et al.*, 2009). Whether brachypterous or not, groups of flightless species and their relatives often occur close to one another in the Hawaiian Islands, in a variety of habitats of known age.

One remarkable example of insect flightlessness in the Hawaiian Islands is in *Thyrocopa* (Lepidoptera: Xyloryctidae: Xyloryctinae), an endemic genus with at least 31 species (Medeiros, 2009). *Thyrocopa* includes two known flightless species, *T. apatela* (Walsingham) and *T. kikaelekea* Medeiros. These diurnal species are sometimes called 'grasshopper moths' because they locomote by jumping. *Thyrocopa apatela* occurs at high elevations on Haleakala volcano on the island of Maui (Zimmerman, 1978; Medeiros, 2009), while *T. kikaelekea* occurs at similar elevations on Mauna Kea volcano on Hawaii Island (Medeiros, 2008). The habitats are characterized by high winds, scattered vegetation, rocky soils, low humidity, extreme daily and seasonal temperature fluctuations, and a lack of native avian predators (Howarth, 1987; Medeiros, 2008). These habitats also cover a small geographic area, and are in a sense islands of habitat on top of actual oceanic islands.

Flightlessness and associated brachyptery in *T. apatela* and *T. kikaelekea* are found in both sexes. This is remarkable, as flightlessness tends to be limited to females in flightless Lepidoptera (Sattler, 1991; Wagner & Liebherr, 1992), probably because there is strong selection for male flight ability so that males can approach females and track pheromone plumes (Sattler, 1991). Male flightlessness in the Lepidoptera only occurs in areas with very high winds, such as small islands and coastal dunes (Powell, 1976; Sattler, 1991). *Thyrocopa apatela* and *T. kikaelekea* join a group of only c. 25 Lepidoptera species world-wide in which both males and females are brachypterous and flightless (Sattler & Wojtusiak, 2000).

In this paper, we use *Thyrocopa* to examine whether two flightless species originated as a result of the diversification of a flightless ancestor, or whether each species evolved flightlessness independently, thereby suggesting a link between alpine areas and the evolution of flightlessness (Roff, 1990, 1994). Specifically, we use a phylogenetic analysis of the *Thyrocopa* to determine whether *T. apatela* and *T. kikaelekea* evolved flightlessness independently of one another, and whether alpine areas are associated with the evolution of flightlessness. By presenting a phylogenetic hypothesis for the entire genus, we are also able to add to the present understanding of biogeographic patterns in the Hawaiian Islands. Dispersal patterns on island chains have attracted considerable recent attention as workers have attempted to elucidate recurrent patterns of island colonization (Jordan *et al.*, 2003; Price, 2004; Shapiro *et al.*, 2006; Magnacca & Danforth, 2007; Short & Liebherr, 2007; Cowie & Holland, 2008; Nitta & O'Grady, 2008; Percy *et al.*, 2008; Rubinoff, 2008; Givnish *et al.*, 2009); for example, the 'progression rule' hypothesis posits that taxa generally island-hop from older to younger islands (Wagner & Funk, 1995). *Thyrocopa*, unlike many Hawaiian taxa, are found both on the Northwestern Hawaiian Island chain (NWHI), which stretches over 1500 km to the north-west of the main islands, and on the 'main' Hawaiian Islands. Therefore, in addition to providing insights into the evolution of flightlessness, this group provides an excellent opportunity to explore patterns of island colonization and diversification and to determine whether island size and age are correlated with

numbers of endemic species (Ricklefs & Bermingham, 2008; Gillespie & Baldwin, 2010).

MATERIALS AND METHODS

Specimen sampling

We collected, or obtained by loan, 23 of the 31 recognized *Thyrocopa* species from nine islands: Necker and Nihoa islands in the NWHI, and Kauai, Oahu, Molokai, Maui, Lanai, Kahoolawe and Hawaii islands (see Fig. 1 for map); most of the species we did not collect are presumed extinct. Except for the flightless species (*T. apatela* and *T. kikaelekea*), most individuals were collected at night using a blacklight and white sheet set up in the forest, although some were collected by hand-net, while perching or flying.

The taxonomic position of *Thyrocopa* has been debated in the literature: some authors place it in the Oecophoridae (Zimmerman, 1978) and others in the Xyloryctidae (Hodges, 1999); even the status (whether it is a family or a subfamily) and placement of Xyloryctidae are unclear (Hodges, 1999; Kaila, 2004). Therefore, seven outgroup taxa from various groups were selected for this study: *Stoerberhinus testaceus* (Gelechiidae), *Carcina quercana*, *Stathmopoda pedella* and *Phaeosaces coarctatella* (Oecophoridae), an unidentified Blastobasini species in the Blastobasidae, and *Cryptophasa sarcoxantha* and *Maroga melanostigma* (Xyloryctidae). *Stoerberhinus testaceus* was selected as the outgroup when analysing the phylogenetic dataset (see below), because Gelechiidae are likely to be outside the rest of the taxa in our study (other outgroups plus *Thyrocopa*) (Kaila, 2004). The taxonomy of *Thyrocopa* itself follows Medeiros (2009).

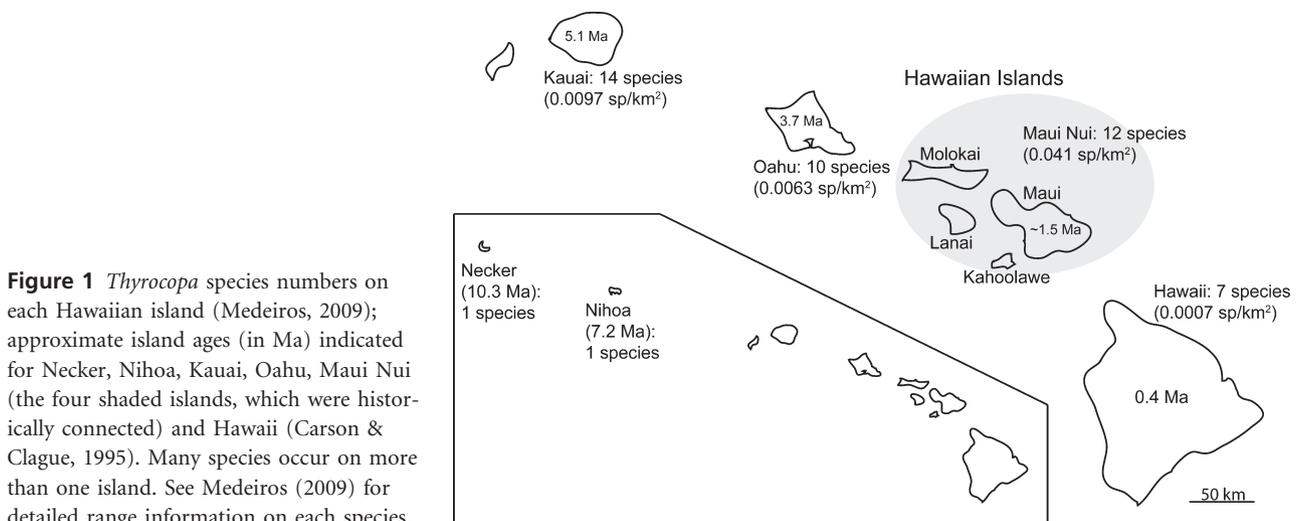
Molecular methods

We extracted DNA from one to three legs of recently killed specimens, which had been stored in 100% ethanol for no longer than 2 years, using Qiagen DNeasy Tissue Kits (Qiagen, Valencia, CA). For older specimens, we extracted DNA

from legs directly removed from pinned moths; the maximum age of dried specimens that yielded usable DNA by this method was four years. Three primer pairs (see Appendix S1 in Supporting Information) were used to sequence a fragment of one mitochondrial gene, cytochrome *c* oxidase subunit I (COI), and fragments of two nuclear genes, *wingless* and elongation factor 1 α (EF1 α), which have proved useful in previous studies of closely related groups of Lepidoptera (Brower & DeSalle, 1998; Monteiro & Pierce, 2001; Warren *et al.*, 2008). To amplify COI, we used the following polymerase chain reaction (PCR) protocol: 40 cycles of 95 °C (30 s)–46 °C (45 s)–72 °C (60 s). To amplify *wingless* and EF1 α , we used the following protocol: 40 cycles of 95 °C (30 s)–55 °C (30 s)–72 °C (45 s). All PCR products were purified using ExoSapIt, cycle-sequenced, and sequenced using an Applied Biosystems 3730 DNA Analyzer (Applied Biosystems, Foster City, CA). Sequences for three outgroup species (*C. sarcoxantha*, *C. quercana* and *S. pedella*) were taken from Mutanen *et al.* (2010). A list of specimens is included in Appendix S2.

Phylogenetic analysis

Every one of the 63 individuals in the ingroup was successfully sequenced for each of the three gene fragments, with these exceptions: 07b55 was not sequenced for *wingless*, and la70 was not sequenced for EF1 α . For the seven outgroup taxa, all individuals were successfully sequenced for all gene fragments, except *wingless* for *S. testaceus*, *P. coarctatella*, *M. melanostigma* and the Blastobasini species, and EF1 α for *C. sarcoxantha*. On several occasions, we included more than one individual from a species in our analysis. Although species and individuals within a species may sometimes evolve at very different rates and cause problems in estimating phylogeny (see, for example, Ho *et al.*, 2005), in most cases we included multiple individuals from a species only when they represented differing populations, either because they lived on different islands or because they had distinctive enough wing patterns so as to call into question their species determination. In the case of *T. apatela* and *T. kikaelekea*, we purposefully included multiple



individuals from these species in order to test each species' monophyly.

We edited sequences and checked alignments using SEQUENCHER 4.6 (Genecodes Corporation, Ann Arbor, MI). To determine whether we could use a concatenated dataset for final phylogenetic analyses, we tested each single gene fragment's dataset by analysing it using the Akaike information criterion (AIC) in MODELTEST 3.7 (Posada & Crandall, 1998). For COI, MODELTEST selected GTR + I + Γ ; for *wingless*, GTR + I; for EF1 α , GTR + I + Γ . We therefore used the GTRGAMMA model in RAXML 2.2.3 (Stamatakis, 2006) to estimate a phylogeny using each gene's dataset independently, because in RAXML the GTRGAMMA model is a close approximation of all the models chosen for each single gene's dataset. We estimated node confidence from each of these datasets by performing 200 nonparametric bootstrap pseudoreplicates. Results of this analysis showed that, except for a very few individuals within a species, no contradictory nodes with a bootstrap support value over 50 were supported in any dataset. Therefore, because the placement of all species in each single gene's dataset was congruent, we concatenated the dataset for final phylogenetic analyses.

To obtain a parsimony tree with the concatenated dataset, we used a PAUP* 4.0b10 (Swofford, 2002) heuristic search (addition sequence = random; number of replicates = 1000; swapping = tree bisection–reconnection (TBR), no limit on 'maxtrees'). Also using PAUP*, we performed 200 nonparametric bootstrap pseudoreplicates of the dataset in order to estimate node support ('maxtrees' = 1000).

To obtain a tree using Bayesian inference, we used MRBAYES 3.1.1 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) with the GTR + I + Γ model of DNA sequence evolution we had estimated for the concatenated dataset using MODELTEST. We partitioned the dataset for each gene and estimated the parameter distributions for each partition independently ('unlinked'). We ran two sets of four chains simultaneously, for 4×10^6 generations each, with a tree sampled every 100 generations. A plot of tree likelihood versus generation number reached stationarity after *c.* 100,000 generations, and we discarded this number of trees as 'burn-in'. The measures of effective sample size (ESS) for each parameter were significant (>200). We then computed a consensus tree with the remaining trees and determined posterior probabilities for each clade based on the proportion of trees in which that particular clade occurred.

Determining divergence times after phylogenetic analysis

To estimate divergence times within our dataset, we used BEAST 1.4.8 (Drummond & Rambaut, 2007). At least one calibration point is required for estimating absolute divergence times. When dealing with biogeographic information, as opposed to fossils, this calibration point must be chosen with caution because association between cladogenesis and geological events is difficult to prove. However, 'hot-spot' archipel-

agos provide a relatively good opportunity to calibrate rates of molecular change based on the geological age of the islands. Assumptions we used were (1) that the branching pattern in the phylogeny parallels the timing of island formation, and (2) that the divergence between sister taxa does not greatly predate the formation of the colonized younger island (Fleischer *et al.*, 1998). Baldwin & Sanderson (1998) have cautioned against the use of internal calibration points for dating evolutionary events in hot-spot archipelagos because errors are greatly magnified deeper within the tree. Additional sources of error can arise from sampling error, extinction of lineages, and high levels of diversity present in the common ancestral population (Emerson *et al.*, 2000).

Based on our assumptions, we selected nodes to date where there was a clear progression of older to younger islands for populations or species, based on our Bayesian phylogenetic analysis. We then calibrated those nodes using the maximum age of the youngest island (Carson & Clague, 1995) involved during the relevant splitting event. Because dates of Hawaiian islands have some margin of error, and because we were not sure how soon after island formation *Thyrocopa* would have colonized the younger island, we used a normal distribution in BEAST when calibrating those nodes. None of the nodes we calibrated was within the 'windswept clade' (see Results), because no species or population within that clade exhibited an older–younger island progression. We selected three nodes, representing both relatively young and relatively old calibrations within the Hawaiian Islands. Other than these nodes, we did not inform BEAST of any phylogenetic structure, instead allowing the program to infer phylogenetic relationships based on divergence times between taxa.

The nodes selected for dating were the *T. indecora* clade, calibrated at 1.32 Ma with the formation of Maui (SD = 0.25 Myr); the *T. indecora* + *T. albonubila* clade, calibrated at 3.7 Ma with the formation of Oahu (SD = 0.5 Myr); and the *T. alterna* clade, calibrated at 0.43 Ma with the formation of Hawaii (SD = 0.25 Myr); these nodes are marked with stars on the BEAST tree (ages are from Carson & Clague, 1995). Our BEAST run was based on a file generated with the user interface 'BEAUTI', and settings were default values except for the following: Data menu – dates specified as years before present; Model menu – base frequencies estimated, site heterogeneity model gamma + invariant sites, did not fix mean substitution rate, molecular clock model uncorrelated lognormal; Priors menu – tree prior: Yule speciation. We ran four independent chains for 10,000,000 generations each, sampling after every 10,000 generations, and discarded the first 10% of the samples in each chain as 'burn-in'. We evaluated the posterior convergence using TRACER 1.4 (<http://beast.bio.ed.ac.uk/Tracer>) and then concatenated the four runs into one final tree estimate, with node ages estimated as the mean of the 95% highest posterior density (HPD) value.

For comparison, we also estimated the age of several nodes based on Brower's (1994) molecular clock estimate of 2.3% divergence per million years in Lepidoptera COI, using only our COI dataset.

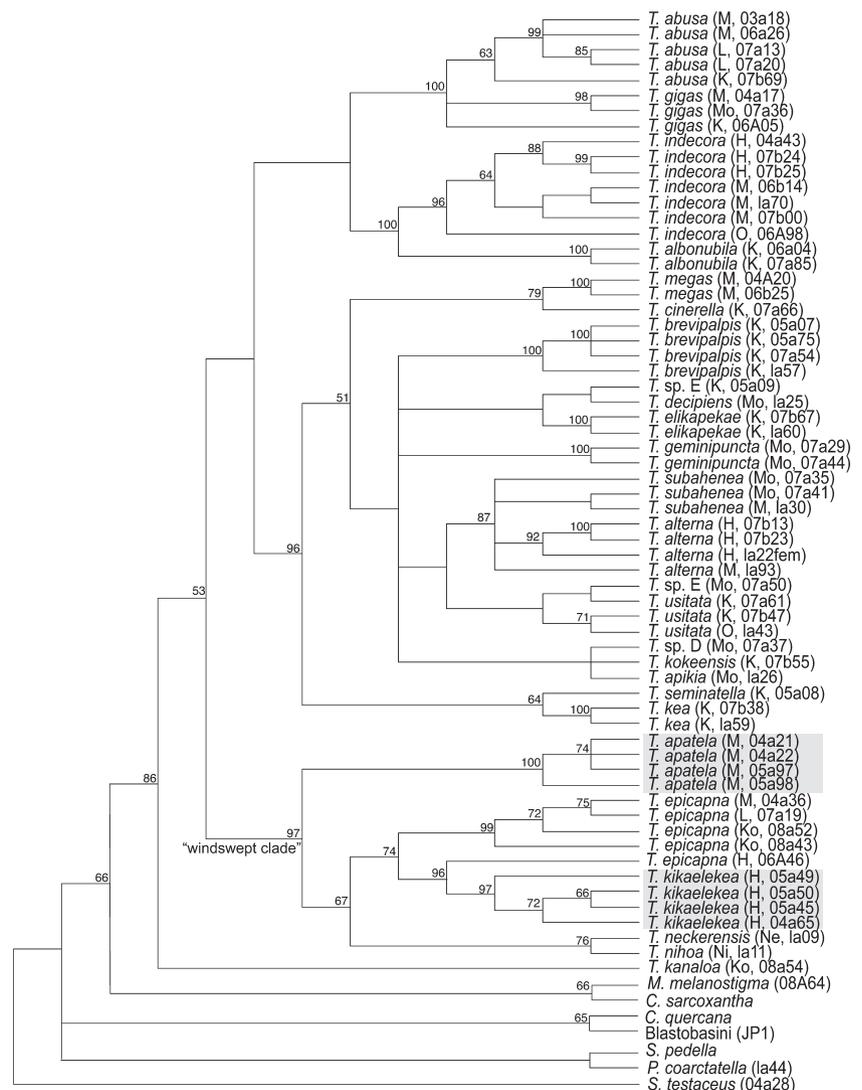
RESULTS

Phylogenetic analysis

Using parsimony, we found 1783 most-parsimonious trees, with treelength = 1417, consistency index (CI) = 0.495, retention index (RI) = 0.732, and rescaled consistency index (RC) = 0.36, the strict consensus shown in Fig. 2. The Bayesian analysis was found to reach convergence after *c.* 9.5 million generations, and one million generations were eliminated as burn-in, giving the tree illustrated in Fig. 3. The two trees share many topological features: *Thyrocopa* is probably a monophyletic group [bootstrap support (BS) = 86; posterior probability (PP) = 100], and, because it is very closely related to *M. melanostigma* and *C. sarcoxantha* (BS = 68; PP = 100), probably falls within the Xyloryctidae, as hypothesized by Hodges (1999). The Xyloryctidae (or Xyloryctinae) are primarily an Australian group (Common, 1990), suggesting that Zimmerman was correct when he wrote that *Thyrocopa* is probably 'of Austral origin' (Zimmerman, 1978,

p. 932). In the parsimony tree, *T. kanaloa* from Kahoolawe is supported as being sister to all other *Thyrocopa*, while this species is sister to *T. albonubila* + *T. indecora* in the Bayesian tree. A 'windswept' clade (composed of species found in dry, rocky, windy habitats; see Discussion for explanation), containing the two NWHI species, plus *T. epicapna* and the two flightless species, *T. apatela* and *T. kikaelekea*, is supported in each tree. Other than the placement of *T. kanaloa*, no topological features in the parsimony and Bayesian trees contradict each other, except for several individuals within species (and for the two individuals sequenced for *T. sp. E*, which may represent two new species), although the number of nodes with support varies somewhat between tree-building methods. Both methods suggest an independent loss of flight in *T. apatela* and *T. kikaelekea*, because these species are not sister to one another (this conclusion is also supported by morphology; see Medeiros, 2009). Instead, *T. kikaelekea* split from the Hawaii population of *T. epicapna*, rendering the latter a paraphyletic species (or, possibly, the Hawaii Island individual, 06A46, represents a new, cryptic species).

Figure 2 Parsimony tree, strict consensus of 1783 trees, for *Thyrocopa* from the Hawaiian Islands. Bootstrap proportions of over 50% are shown. Flightless species are shaded. Ne, Necker; Ni, Nihoa; K, Kauai; O, Oahu; Mo, Molokai; M, Maui; L, Lanai; Ko, Kahoolawe; H, Hawaii Island.



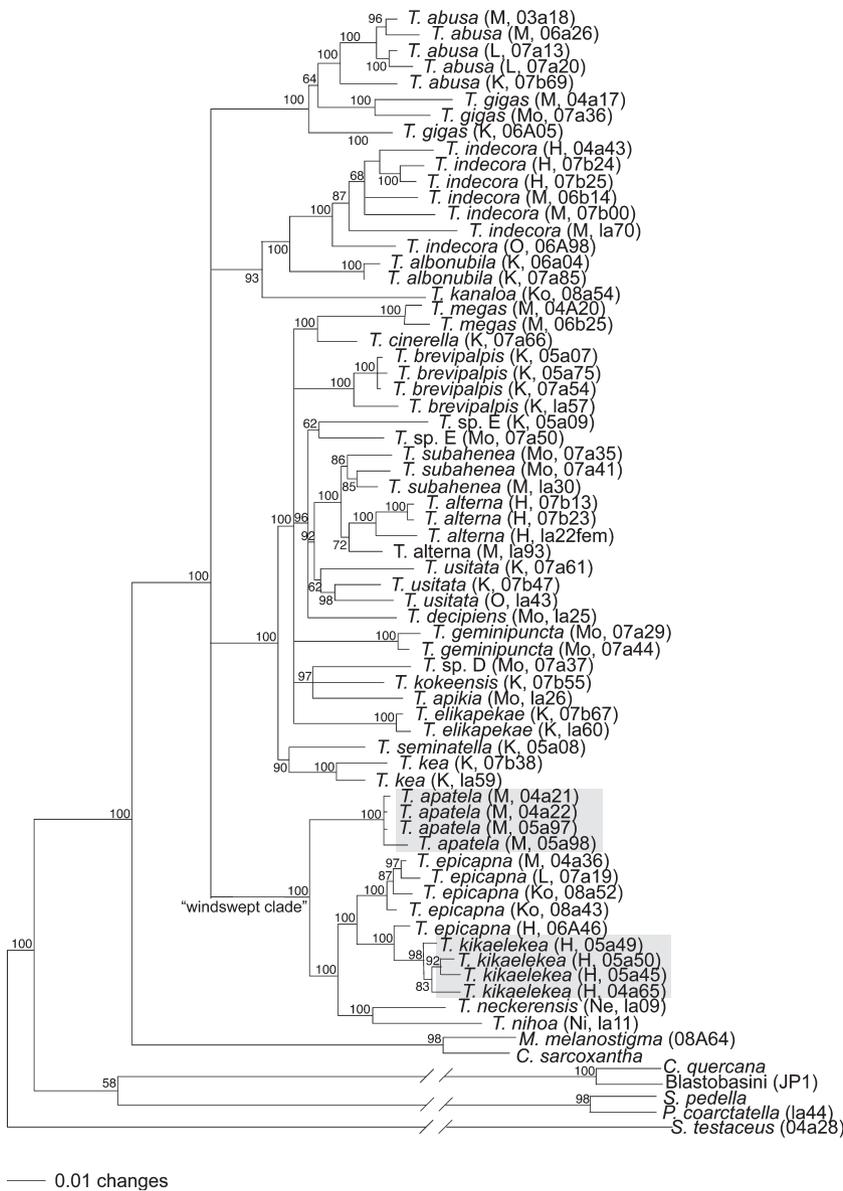


Figure 3 Bayesian tree, with branch lengths indicated, for *Thyrocopa* from the Hawaiian Islands. Posterior probability values of over 50 are shown. Flightless species are shaded. Ne, Necker; Ni, Nihoa; K, Kauai; O, Oahu; Mo, Molokai; M, Maui; L, Lanai; Ko, Kahoolawe; H, Hawaii Island.

Divergence times

Divergence times, in millions of years ago (Ma), along with bars showing the 95% HPD, are shown in Fig. 4, although the bar for the most ancestral node (10.54 Ma) has been deleted (the values for 95% HPD for this node are 6.33–15.19 Ma). Phylogenetic structure estimated using BEAST was largely congruent with that of our other phylogenetic estimates. The only differences were the positions of several species in the non-‘windswept’ clades, generally among recently divergent species, including differences in the branching pattern of populations of *T. indecora*, one of the nodes we used for calibration based on our Bayesian analysis.

Use of Brower’s (1994) molecular clock estimate resulted in the divergence times of several nodes having similar values to those in BEAST: the ‘windswept clade’ is estimated at 2.5 Ma (based on the distance between la11 and 04A21); *T. kikaelekea* split from *T. epicapna* on Hawaii Island 1.0 Ma

(distance between 06A46 and 05A45). Values for the three main subclades in which the basal taxon was on Kauai are 2.1 Ma (*T. gigas* 06a05 to *T. abusa* 03a18), 3.1 Ma (*T. albonubila* 07a85 to *T. indecora* 04a43) and 2.2 Ma (*T. kea* la59 to *T. alterna* la22fem).

DISCUSSION

The results provide insights into (1) biogeographic patterns and (2) the evolution of flightlessness in *Thyrocopa*.

Biogeographic patterns within *Thyrocopa*

The phylogenetic analyses (Figs 2–4) indicate four major clades of *Thyrocopa*, all of which inhabit wet forest except for a ‘windswept clade’, which includes all species in exposed/high-elevation habitats: *T. kikaelekea*, *T. epicapna*, *T. nihoa* and *T. neckerensis*.

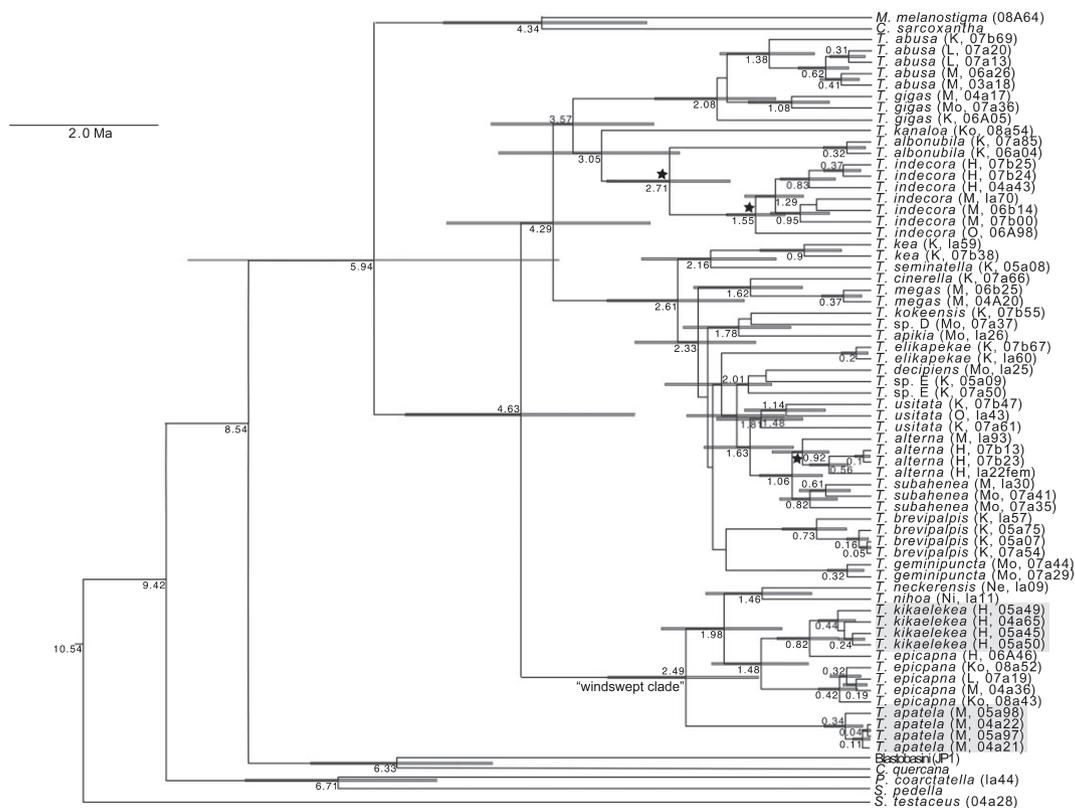


Figure 4 Divergence times for *Thyrocopa* from the Hawaiian Islands (in Ma). Node ages are estimated using BEAST. Bars are 95% confidence intervals; missing bars indicate low support values for a node. Stars indicate calibration points; see text for details. Flightless species are shaded. Ne, Necker; Ni, Nihoa; K, Kauai; O, Oahu; Mo, Molokai; M, Maui; L, Lanai; Ko, Kahoolawe; H, Hawaii Island.

Placement of *T. kanaloa*

Although parsimony suggests that *T. kanaloa* from the relatively young island of Kahoolawe is sister to the rest of the Hawaiian *Thyrocopa*, this placement was not supported in our Bayesian or BEAST analyses, nor in our original likelihood analysis using RAXML (see Materials and Methods). Although unlikely, if *T. kanaloa* is indeed sister to the rest of *Thyrocopa*, possible explanations are (1) that *T. kanaloa* is a surviving lineage of an independent colonization to the Hawaiian Islands (multiple invasions to the islands have been observed in several other taxa: Gillespie *et al.*, 1994; Cowie & Holland, 2008); or (2) that *Thyrocopa* colonized the Hawaiian Islands once, and there has been subsequent extinction of lineages closely related to *T. kanaloa*.

Progression-rule hypothesis

A progression from older to younger islands, as predicted by the progression rule (Wagner & Funk, 1995), is not found in the phylogeny of *Thyrocopa* overall. However, relationships within three major subclades (although the 'windswept' clade is an exception) are consistent with the pattern within the current high islands, with species on Kauai generally sister to species or populations on younger islands. Estimates of node ages suggest that the basal split in each of these three clades

occurred when Kauai and Oahu were the youngest islands in the chain. It appears that each lineage subsequently dispersed down the island chain after the younger islands formed (island ages in Fig. 1). The estimate by BEAST that *Thyrocopa* split from other Xyloryctidae at 5.94 Ma suggests that *Thyrocopa* colonized the Hawaiian Islands shortly before the formation of Kauai, although increased taxon sampling of non-Hawaiian Xyloryctidae would improve this estimate.

Thyrocopa is now one of a few groups to occur on, and be sampled from, both the main Hawaiian Islands and the NWHI (see also Price, 2004; Cowie & Holland, 2008; Rubinoff, 2008; Eggert *et al.*, 2009; Shapiro *et al.*, 2006). However, unlike *Banza* (Shapiro *et al.*, 2006), the two species of *Thyrocopa* that occur on the NWHI, *T. neckerensis* and *T. nihoa* of the 'windswept clade', have arisen through back-colonization from the younger high islands. Indeed, the strongest predictor of where *Thyrocopa* species occur seems to be habitat type, because *T. neckerensis* and *T. nihoa* on the NWHI are sister to species from exposed – although high-elevation – sites on the main islands. All other *Thyrocopa* (excluding *T. kanaloa* from Kahoolawe) are found in wet or mesic forest habitats.

Number of species versus island age

Assuming that *Thyrocopa* has been in the Hawaiian Islands since approximately the formation of Kauai (5.1 Ma), it is

possible to use the island chronology to provide 'snapshots' of species diversification over the history of the islands. Gillespie & Baldwin (2010) have shown that, for lineages that have been in the islands at least throughout the existence of the current high islands (i.e. *c.* 5 Ma), the maximum number of species per unit area for the very large radiations (> *c.* 60 species) in the Hawaiian Islands generally occurs on islands of intermediate age (Maui Nui or Oahu), while smaller radiations (*c.* 40 or fewer species) show a steady increase in the number of species per unit area with island age (for example, *Megalagrion* damselflies and *Orsonwelles* spiders, as well as some plants: Jordan *et al.*, 2003; Price, 2004; Gillespie & Baldwin, 2010). *Thyrocopa* is consistent with this pattern: excluding the small islands of Necker and Nihoa, Kauai is home to the most species of *Thyrocopa* per unit area of any Hawaiian island, followed by intermediate numbers on Oahu and Maui Nui, and a lower number on Hawaii Island (Fig. 1). Factors driving diversification in this group remain unknown, as *Thyrocopa* are not host-plant specialists (Medeiros, 2009).

The evolution of flightlessness in *Thyrocopa*

Flightlessness evolved independently in *T. apatela* and *T. kikaelekea*, following independent alpine invasions on Maui and Hawaii islands, respectively. It is unlikely that flightlessness evolved only once, followed by a regaining of flight ability in *T. nihoa* + *T. neckerensis*, and *T. epicapna*, for several reasons. First, invoking two losses of flight is more parsimonious than at least three origins of flight. Second, *T. epicapna* is paraphyletic (Figs 2–4) and would have had to have gained flight ability independently on at least two islands (Kahoolawe and Hawaii islands at a minimum). Third, *T. apatela* and *T. kikaelekea* both appear to be in the early stages of loss of flight ability: not only are some *T. apatela* individuals macropterous (Medeiros, 2009), but both *T. apatela* and *T. kikaelekea* locomote by jumping with outstretched, possibly low-amplitude, flapping wings (Medeiros, 2008).

Evidently, alpine living is related to flightlessness in *Thyrocopa*. The three other species that form a 'windswept clade' within *Thyrocopa*, namely *T. epicapna*, *T. nihoa* and *T. neckerensis*, all retain the ability to fly, while living in habitats that are very windy, dry, rocky, and sparsely vegetated, but differing markedly from alpine areas in elevation and therefore temperature. No other *Thyrocopa* species commonly occurs in the dry, windy, rocky areas of the Hawaiian Islands, in either low-elevation coastal habitats or alpine habitats; other than the members of the 'windswept clade' (and *T. kanaloa*), all *Thyrocopa* live in wet or mesic habitats. And although two volant species have been collected at high elevations (*T. alterna* and *T. indecora*), they are not abundant there, were possibly blown up to those elevations by wind, and are much more commonly found at lower elevations (Medeiros, 2009). Therefore, some difference or combination of differences unique to the alpine habitats appears to be the factor that increases selection for loss of flight ability.

High wind is hypothesized to lead to flightlessness, because the potential for being blown out to sea, leading to selection against passive dispersal, is of prime importance in alpine (Sattler & Wojtusiak, 2000) and island (Darwin, 1859; Carlquist, 1965) habitats. Darwin suggested that flightless insects would have a lower chance than flighted insects of being blown off their islands in the wind. For alpine *Thyrocopa*, being passively dispersed could be a strong disadvantage, because individuals could be blown out of the particular habitat type to which they are presumably adapted. (However, passive dispersal could also be advantageous for these insects. For alpine *Thyrocopa*, being passively blown by wind to areas where plant debris builds up under rocks could ensure that larvae were well fed: Howarth, 1979, 1987). High winds could also disrupt pheromone signalling (Sattler, 1991; Sattler & Wojtusiak, 2000), another reason that flight may not confer benefits to alpine *Thyrocopa*. Like all other Lepidoptera species with male brachyptery, *T. apatela* and *T. kikaelekea* live in areas with consistently high winds (Sattler, 1991; Sattler & Wojtusiak, 2000). This suggests that high winds play a selective role in reducing the ability to fly. However, members of the same clade are fully flighted under similar windy conditions in the NWHI. Therefore, it appears that wind alone does not explain the loss of flight in *Thyrocopa*. Rather, flight loss appears to be tied to alpine living, perhaps in combination with the windswept environment. Wings may be used by flightless species to stabilize the body during jumping (Sattler, 1991), and outstretched wings allow some flightless moth species to control their descent trajectory (Harper, 1990). This may be one reason why brachypterous wings are maintained in most flightless Lepidoptera (Sattler, 1991).

The historical scarcity of volant predators in the alpine areas of Haleakala and Mauna Kea would have meant that diurnal alpine *Thyrocopa* species would not have had to travel large distances to escape from immediate danger (although *T. neckerensis* and *T. nihoa* are nocturnal and should not have had native volant predators when active). Lycosid spiders and carabid beetles, probably the main predators of alpine *Thyrocopa*, could be evaded just as effectively by quickly jumping many centimetres away, and adults of *T. apatela* and *T. kikaelekea* are both able to jump well over 10 cm, sometimes more than 20 cm (M. J. Medeiros, pers. obs.). Another difference between Hawaii's alpine areas and the small atolls of Necker and Nihoa is that, while Necker and Nihoa are warm throughout the year and generally lack severe temperature fluctuations, even on a daily basis, temperature shifts on Haleakala and Mauna Kea are abrupt and dramatic, on both a daily and a seasonal basis. Perhaps the regular cold temperatures, often below freezing, of alpine areas explain the loss of flight of *T. apatela* and *T. kikaelekea*, while *T. neckerensis* and *T. nihoa* rarely experience temperatures cold enough to thwart flight.

The NWHI are much older than Maui and Hawaii islands (Fig. 1). Based on the phylogenetic reconstruction, *T. neckerensis* and *T. nihoa* probably colonized their respective islands no earlier than the time of formation of Maui, 1.32 Ma (see Fig. 4). Both *T. kikaelekea* and *T. apatela* appear to have lost

flight ability in less than 0.43 Myr and 1.32 Myr, the respective age of the alpine habitats in which they occur, suggesting that loss of flight evolved quickly in Hawaiian alpine ecosystems and that selection pressures on Necker and Nihoa Islands are appreciably different from those in Hawaiian alpine systems.

Wagner & Liebherr (1992) point out that the interactions between a number of environmental factors make it difficult to determine why any given insect is flightless. It is possible that unique combinations (discussed in general terms by Carlquist, 1965), such as cold temperatures in combination with high winds and reduced predation pressure from volant predators, or difficulties in flight brought about by reductions in air density at high altitudes (Dudley, 2000), may lead to conditions where flight is inefficient and not necessary for survival and reproduction. In fact, flightless individuals may be at an advantage because energy that would otherwise be spent on thoracic musculature or wing flapping may be devoted to reproduction, especially in females (Roff, 1986, 1990; Roff & Fairbairn, 1991; Zera *et al.*, 1997; Harshman & Zera, 2007; Ikeda *et al.*, 2008; Saglam *et al.*, 2008). A combination of relaxed predation pressure along with high winds has been suggested to lead to the flightless and brachypterous condition in both sexes of the California sand dune moth *Areniscythis brachyptervis* Powell (Scythrididae) (Powell, 1976). Future research to resolve the phylogenies of groups with several flightless species, such as the New Zealand *Kiwaia* moths (Sattler, 1991), will add to our understanding of the ecological correlates of flightlessness in Lepidoptera.

ACKNOWLEDGEMENTS

We thank three anonymous referees for comments that greatly improved the manuscript, and Jordana Anderson, Sam Aruch, Sara Backowski, Randy Bartlett, Gordon Bennett, Jeremy Dresel, Robert Dudley, Betsy Gagné, Jon Giffin, the Evolab at UC Berkeley, Will Haines, Ryan Hill, Frank Howarth, Kevin Jenkins, Raina Kaholoa'a, Adam Leaché, David Medeiros, Andrew Mitchell, Shepherd Myers, Steve Montgomery, Marko Mutanen, Pete Oboyski, Patrick O'Grady, Kevin Padian, Bonnie Ploger, Jerry Powell, Kari Roesch Goodman, Klaus Sattler, Sean Schoville, Wayne Souza, Kevin Tuck, Liz Wang, the Molokai TNC, the staff at Kokee State Park, and the Kahoolawe Island Reserve Commission for help with collecting, logistics and advice. This research was supported in part by the University of California, Berkeley, Department of Integrative Biology, UC Museum of Paleontology, the NSF GK-12 Exploring California Biodiversity grant, the Schlinger Foundation, and the Margaret C. Walker Fund for teaching and research in systematic entomology. The work presented here represents a portion of M.J.M.'s PhD dissertation research at the University of California, Berkeley.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Primers used in this study.

Appendix S2 Specimens included in the phylogenetic analysis.

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BIOSKETCHES

Matthew Medeiros is a research associate in the Department of Entomology at the Smithsonian Institution in Washington, DC, and teaches at the Landon School in Bethesda, MD. He recently earned his PhD from the University of California, Berkeley, where he studied the evolution of flightlessness in cave and alpine Hawaiian moths. His research interests include Hawaiian biogeography, insect flightlessness and Lepidoptera taxonomy.

Rosemary Gillespie is Director of the Essig Museum of Entomology and Professor in Environmental Science at the University of California, Berkeley, where she holds the Schlinger Chair in Systematic Entomology. Her main research interests are the biogeographic patterns and ecological and evolutionary processes that govern the formation of populations, species and communities on isolated landmasses. Her work focuses on the evolution of Hawaiian spider fauna.

Editor: Şerban Procheş