PACIFIC SCIENCE Early View
A Quarterly Devoted to the
Biological and Physical Sciences of the Pacific Region

Can ornithophilous Hawaiian lobeliads produce seeds in the absence of pollinators? A test using *Clermontia kakeana* and *Cyanea angustifolia* (Campanulaceae)

By Coleen Cory, Richard Pender* and C. Eugene Jones

Abstract

The native Hawaiian bird pollinated flora is primarily composed of five ornithophilous lobeliad genera, collectively containing approximately 137 species. Historically, these genera were believed to have been pollinated by at least some of the ten specialist nectarivorous bird species endemic to Hawaii. However, since human colonization, both bird and ornithophilous native plant species have undergone widescale declines and extinctions, resulting in the potential loss of pollination service for a significant proportion of the native flora. In an attempt to assess if lobeliad species can produce viable seeds in the absence of pollinators, two pollination treatments (open-control and pollinator exclusion) were applied to two Hawaiian lobeliad species (*Clermontia kakeana* Meyen and *Cyanea angustifolia* (Cham.) Hillebr., in single populations of each species on Oahu. In each lobeliad species, mean seed counts were not significantly different in fruits resulting from open pollinated and pollinator excluded flowers. This suggests that both species are capable of autogamy and can produce seeds in the absence of pollinators.

Corresponding author. E-mail: thatplantguy@gmail.com

Pacific Science, vol. 69, no. 2
October 20, 2014 (Early view)

INTRODUCTION

The Hawaiian lobeliads represent one of the most remarkable adaptive radiations in the Angiosperms (Givnish et al. 2009). Composed of six genera, the approximately 140 species (taxonomy follows Lammers 2007 a, b, Lammers 2009) of herbs, shrubs, trees and stout caudiciforms evolved, following a single colonization event, approximately 13 million years ago (mya), to fill a diverse range of habitat niches present on the main islands of the Hawaiian archipelago (Givnish et al. 2009). Despite this morphological diversity, five Hawaiian lobeliad genera, and almost all lobeliad species (n = *ca.*137 spp.), possess floral features congruent with an ornithophilous pollination syndrome (Lammers and Freeman 1986, Pender et al. 2014). Based on our current understanding, ornithophilous Hawaiian lobeliads are believed to have been pollinated by nectarivorous Hawaiian Drepanidinae (Hawaiian honeycreepers) and Mohoidae (previously classified as Hawaiian Honeyeaters, *see* Fleisher et al. 2008) (Perkins 1895, 1901, 1903, Munro 1960, Speith 1966, Lammers and Freeman 1986).

The congruence between the curved bills of nectarivorous honeycreeper species, particularly in the genera *Drepanis* and *Vestiaria,* and the flowers of lobeliad species, combined with casual observations of honeycreepers foraging from lobeliad flowers (Cassin 1858, Wilson 1890, Rothschild 1893-1900, Perkins 1895, 1903, Bryan 1908, Amadon 1950, Munro 1960, Spieth 1966, Richards and Bock 1973, Berger 1981) has led to much speculation regarding co-evolution between these potential mutualists (Perkins 1903, Carlquist 1980, Lammers and Freeman 1986, Givnish et al. 1995). Perkins (1901) hypothesized that lobeliads were dependent upon honeycreepers for successful reproduction. Spieth (1966), Stone (1967), and Ehrendorfer (1979) similarly speculated about this relationship. However, Rock (1919) and St. John (in Amadon 1950) suggested that honeycreepers are important, but not essential, for the pollination of some lobeliad species. Interestingly, the role that Mohoidae may have played as lobeliad pollinators has received little attention, despite published observations of several *Moho* species visiting the flowers of lobeliad species (Wilson 1890, Perkins 1903, Munro 1960) and the more recent evidence that suggests that lobeliads and Mohoidae coexisted in Hawaii for approximately 7 million years before the colonization of Hawaiian honeycreepers (Fleisher and McIntosh 2001, Fleischer et al. 2008, Givnish et al. 2009).

Due to habitat destruction and the introduction of invasive species following the colonization of Hawaii by humans, two of the five specialist nectarivorous honeycreeper species and all Mohoidae species are extinct (reviewed in Banko and Banko 2009). The remaining extant specialist and generalist nectarivorous passerine species (n = 7 spp.) have undergone distributional range reductions (Banko and Banko 2009, Gorresen et al. 2009). Primarily due to the avian diseases, avian pox (*Poxvirus avium*) and avian malaria (*Plasmodium relictum*) that are transmitted by introduced mosquitoes (principally *Culex quinquefasciatus* Say), potential interactions between lobeliad species and the remaining nectarivorous honeycreeper species (and particularly ‘i‘iwi) are mostly limited to higher elevation habitats (1100m and higher) on the main Hawaiian Islands (Warner 1968, Fancy and Ralph 1998, Gorreson et al. 2009, R. Pender, unpublished data). In addition, Japanese white eye, a generalist species that was introduced to Hawaii in 1929 (van Riper 2000), is a substitute pollinator for some lobeliad species (Aslan et al. 2014), but nectar robs (consumes floral nectar without contacting reproductive organs) the flowers of other species (Gardener and Daehler 2006, Pender 2013, Aslan et al. 2014).

Given the decline of Hawai‘i’s native bird pollinators and the uncertain role of Japanese white eye as substitute pollinators for the wider Hawaiian lobeliad lineage, the objective of this study was to determine if lobeliad species can produce viable seeds in the absence of pollinators by autogamy (selfing). To answer this question, we excluded pollinators from the flowers of *Cl. kakeana* and *Cy. angustifolia* at a single population of each species on the island of Oahu. Seeds were subsequently counted and tested for viability in fruits resulting from flowers that were bagged and flowers that were open to pollinator visitation.

MATERIALS AND METHODS

Study species

Clermontia kakeana is a large shrub or small tree that grows up to six meters tall. This species occurs on Oʻahu, Molokaʻi, and Maui between 245 and 1100 m in elevation (Wagner et al. 1999). The tubular perianth lobes are pale green on the outer surfaces and green to white on the inner surfaces (Wagner et al. 1999). The flowers usually occur in pairs, with perianths 4.5-5.5 cm long and 0.8-1.4 cm wide (Wagner et al. 1999). The berries are bright orange, sub-globose or oblong, and measure 1.8-3.4 cm long and 1.5-3.4 cm wide (Wagner et al. 1999). *Clermontia kakeana* flowers most heavily in the spring and summer, but some individuals have flowers and fruits present throughout the year (C. Cory pers. obs.).

Cyanea angustifolia is a shrub which reaches 1.5-5 m tall (Wagner et al. 1999). The species occurs in mesic and wet forest on both the Koʻolau and Waiʻanae Mountains on Oʻahu, Molokaʻi, Lanaʻi and West Maui between 150-760 m (Wagner et al. 1999). The flowers are held in 6-25 flowered inflorescences. The corolla is white to greenish white, often tinged pink-purple, 2-3 cm long and 0.2-0.3 cm wide. The berries are purple, globose and 5-10 mm long. Peak flowering typically occurs during late spring and early summer (C. Cory, pers. obs.).

Like all Hawaiian lobeliads, both *Cl. kakeana* and *Cy. angustifolia* are protandrous (Wagner et al. 1999). The anthers and filaments are fused, forming a tube around the stigma and style. Anthers release pollen into the fused stamen tube. Pollen is subsequently expelled out of the stamen apex by the immature stigma lobes as the style elongates. Short, stiff hairs on the tips of the ventral anthers aid in collecting the pollen, allowing the pollen to be brushed onto pollinators. The pollen is then carried to flowers that have passed into the female phase (stigma receptive phase). This phase occurs when the style emerges from the anther tube and the stigma lobes enlarge and spread (Pender, unpublished data).

Study sites

Single populations of *Cl. kakeana* and *Cy. angustifolia* were studied in the southern Koʻolau Mountain Range (Figure 1). The *Cl. kakeana* study site was situated on the northwest slope of Mt. Tantalus at an elevation of 540 m. Average annual rainfall at the site is estimated to be 3702 mm (Giambelluca et al. 2013). At the time that the study was undertaken (1980-1984; Cory 1984), the forest at the site was composed of the native canopy species ʻōhiʻa (*Metrosideros polymorpha* Gaud.) and koa (*Acacia koa* A. Gray), and an understory dominated by alien species such as guava (*Psidium guajava* L.), fiddlewood (*Citharexylum caudatum* L.), thimbleberry (*Rubus rosifolius* Sm.) and palm grass (*Setaria palmifolia* (J. König) Stapf). The *Cl. angustifolia* site was located on Waʻahila Ridge at an elevation of 420 m. Average annual rainfall at the site is estimated to be 3296 mm (Giambelluca et al. 2013). The forest contained scattered mature ʻōhiʻa and koa, while the understory was dominated by strawberry guava (*Psidium cattleianum* Sabine).

<<Figure 1 (map) around here>>

Pollination experiments

Autogamous (bagged) and open-pollinated pollination treatments: To test for autogamy, pollinators were excluded from 46 flowers across six *Cl. kakeana* plants and 157 flowers from 23 inflorescences across seven *Cy. angustifolia* plants using 10 cm^2 pollinator exclusion bags made from mosquito netting (<1 mm^2 gauge). The number of flowers utilized per plant ranged between four and 22 for *Cl. kakeana* and between eight and 37 for *Cy. angustifolia*. Bags were placed over pairs of *Cl. kakeana* buds and entire immature inflorescences of *Cy. angustifolia* and secured with either nylon string or wire twist ties. The proportion of flowers bagged ranged from 10 to 50% of the total number of flowers on any given plant. Open-pollinated (control) flowers were not formally allocated at the time that the autogamous pollination treatment was executed.

However, mature, open-pollinated fruits were randomly collected from the same plants that had flowers bagged for the autogamous pollination treatment. Several additional non-pollination treatment plants from each species were utilized to collect open-pollinated fruits due to low fruit set on the treatment plants.

Fruit collection and seed counting: Fruits resulting from each pollination treatment were collected from the *Cl. kakeana* and *Cy. angustifolia* study plants approximately two to three months after flowering. In the bagged pollination treatment, seeds were counted from fifteen fruits (between two to six per plant) from four *Cl. kakeana* plants and 36 fruits (between four to 16 per plant) from four *Cy. angustifolia* plants. For the open-pollinated treatment, seeds were counted from 18 fruits (fruit collected per plant not recorded) from four *Cl. kakeana* plants and 31 fruits (between three and eight per plant) from five *Cy. angustifolia* plants. Seeds from each treatment fruit were extracted by smearing the fruit on paper to separate the seeds from the fruit pulp. In some fruits, all the seeds were counted and in others either ¼ or ½ of the seeds were counted and then multiplied by two or four, respectively, to calculate total seed counts.

Seed viability: To test seed viability, 15 fruit resulting from bagged flowers and 18 open pollinated fruits, collected from four and five *Cl. kakeana* plants, respectively, were selected. In *Cy. angustifolia*, 36 fruit resulting from bagged flowers (collected from four plants) and 17 open pollinated fruits (collected from three plants) were selected. The number of fruits collected per plant in each treatment ranged between one and eight in *Cl. kakeana* and between three and sixteen in *Cy. angustifolia*. Either all, or a subset of seeds (between 10-500 seeds/fruit) were assessed for viability. In total, 22,852 and 16,339 *Cl. kakeana* seeds and 2,506 and 1,396 *Cy. angustifolia* seeds were counted in the bagged and open pollinated fruits, respectively. Seed viability was primarily assessed based on the gross morphology of seeds; those that were dark, firm and plump were considered to be viable. The seeds were subsequently pooled from the two separate pollination treatments in each separate species from which a small subset were selected

(870 *Cl. kakeana* seeds and 75 *Cy. angustifolia* seeds). These seeds had their seed coats split by gently applying pressure using a scalpel and were subsequently soaked in a 1% tetrazolium solution (Porter et al.1947) for 48 hrs to further verify their viability.

Statistical analysis

In cases where multiple fruits were collected from an individual plant in an individual year, mean seed counts per fruit per plant were first calculated. Anderson-Darling Normality Tests were subsequently used to confirm equal variances. The mean number of seeds per fruit was compared between treatments (open *vs*. bagged) in each lobeliad species using two-sample *t*-tests. Means are presented ± 1 S.D. Statistical analyses were undertaken in Minitab 15 (Minitab Inc. State College, PA, U.S).

RESULTS

Pollination experiments

Autogamous (bagged) and open-pollinated fruit set: Of the 46 *Cl. kakeana* flowers that were bagged prior to opening, all but one formed a mature fruit. Of the 157 *Cy. angustifolia* flowers that were bagged prior to opening, 110 developed into mature fruits. Of the 47 buds that did not set fruit, 28 died before fruit formation, 5 were missing and 14 were still open flowers when the inflorescences were collected.

Autogamous and open-pollinated seed set: There was no significant difference in mean seed counts between fruits from 15 bagged and 18 open-pollinated *Cl. kakeana* flowers (mean seeds per fruit = 2118 ± 864 and mean = 2043 ± 585, respectively; $t = 0.16$, $df = 3$, $p = 0.880$). Similarly, there was no significant difference in mean seed counts between fruits from 36 bagged and 31 open-pollinated *Cy. angustifolia* flowers (mean seeds/fruit = 207 ± 123 and mean seeds/fruit = 214 ± 132, respectively; $t = 0.62$, $df = 7$, $p = 0.56$).

Seed viability: Almost all (99%) of the *Cl. kakeana* and all of the *Cy. angustifolia* seeds resulting from bagged and open pollination treatments appeared to be viable based on gross morphology. Likewise, all of the *Cl. kakeana* and *Cy. angustifolia* seeds from both treatments that were tested with tetrazolium were found to be viable.

DISCUSSION

Based on the results of the pollination treatments, both *Cl. kakeana* and *Cy. angustifolia* appear to be capable of producing seeds by autogamy. Although this study was only undertaken with two species, our results support the earlier propositions of Rock (1919), St. John (in Amadon 1950) and Carlquist (1974), who suggested that pollinators were not necessary for seed production in at least some Hawaiian lobeliad species.

The evolution of autogamy in *Cl. kakeana* and *Cy. angustifolia* may have arisen via different mechanisms. Either the progenitor of Hawaiian lobeliads was self compatible or this breeding system evolved *in situ*. Baker's-Rule (Baker 1955, 1967) states that self compatible, self-pollinating species are better adapted to colonize remote islands as they do not rely upon animal pollinators upon colonization. This scenario is more likely than a self-incompatible species arriving and subsequently undergoing selection towards self compatibility. However, the latter mechanism cannot be categorically ruled out, particularly given that a range of breeding systems are known to occur in non-Hawaiian lobeliads (Young 1982, Johnston 1993, Griffin and Byers 2012).

Two physical mechanisms may facilitate autogamy in the flowers of both lobeliad species. First, the stigma lobes recurve as they mature, in some cases contacting the anther hairs (C. Cory pers. obs.). These stigmas may therefore collect latent pollen attached to the anther hairs. Second, self pollen carried on the immature stigma as the flower passes from the male to the female phase may also potentially pollinate the stigma as it matures. Unpublished studies

(Pender pers. obs.) indicate that the pollen in four additional lobeliad species is viable over the life of the flowers (ca. 7 days), allowing sufficient time for pollination to occur by either mechanism. Detailed studies are needed to pinpoint the underlying mechanism of autogamy in these and other Hawaiian lobeliad species.

Conclusions

This study suggests that both *Cl. kakeana* and *Cl. angustifolia* can produce seeds in the absence of pollinators. The ability to produce seeds via autogamy may be one of the reasons why these two species still persist in mid elevation habitats on Oahu where avian pollinators are either rare or absent (Gorresen et al. 2009). Recent studies by Pender (2013) and Aslan et al. (2014) have found that seven other Hawaiian lobeliad species utilize autogamy as part of a mixed mating system (seeds result from outcrossing and autogamy: Goodwillie et al. 2005). Similar studies utilizing *Cl. kakeana* and *Cl. angustifolia* and other Hawaiian lobeliad species are needed, both to understand the evolution of breeding systems and the pollination ecology of this unique component of the Hawaiian flora.

ACKNOWLEDGEMENTS

CC thanks the Departmental Associations Council of California State University Fullerton (CSUF) for partial funding of this work; the Hawaiʻi Department of Land and Natural Resources for access to roads on Mt. Tantalus; Leo Song (CSUF), Dave Karl (University of Hawaiʻi at Mānoa; UHM) and Charles Lambert (CSUF) for technical assistance; and John Learned and other volunteers who assisted with field work. The authors thank Dr. Clare Aslan, Dr. Don Drake, Dr. Cliff Morden, Lara Reynolds and Dr. Aaron Shiels for providing helpful comments on earlier drafts of the manuscript. RJP gratefully acknowledges the financial support provided by Fulbright New Zealand and the John R. Templin Scholarship.

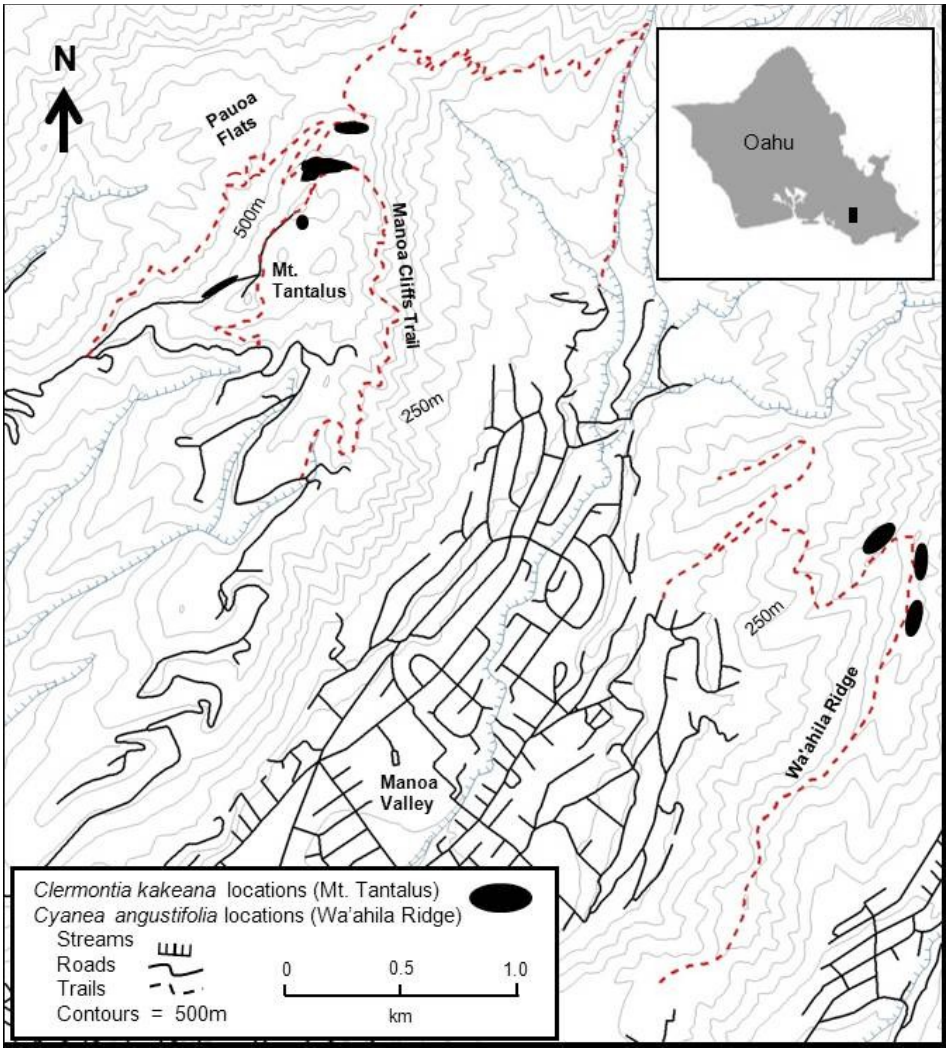

Fig. 1. Locations of the *Cl. kakeana* and *Cy. angustifolia* populations used in the study (created in ArcMap 10 from layers downloaded from State of Hawai‘i Office of Planning web site: http://planning.hawaii.gov/).

LITERATURE CITED

Amadon, D. 1950. The Hawaiian honeycreepers (Aves, Drepanididae). Bull. Am. Mus. Nat. Hist. 95(4): 151-262.

Aslan, C. E., E. S. Zavaleta, B. Tershy, D. Croll, and R. H. Robichaux. 2014. Imperfect replacement of native species by non-native species as pollinators of endemic Hawaiian plants. Conserv. Biol. 28(2): 478-488.

Baker, H. G. 1955. Self-compatibility and establishment after "long-distance" dispersal. Evolution 9: 347-349.

———. 1967. Support for Baker's Law – As a rule. Evolution 21(4): 853-856.

Banko, W. E., and P. C. Banko. 2009. Historic decline and extinction. Pages 25-58 *in* T. K. Pratt, C. T. Atkinson, P. C. Banko, J. D. Jacobi, and B. L. Woodworth, eds. Conservation Biology of Hawaiian Forest Birds: implications for island avifauna. Yale University Press, New Haven and London.

Berger, A. J. 1981. Hawaiian Birdlife. Second Edition. University of Hawai'i Press, Honolulu.

Bryan, W. A. 1908. Some birds of Molokai. Occ. Pap. Bernice P. Bishop Mus. 4(2): 133-176.

Carlquist, S. 1974. Island Biology. Columbia University Press, New York.

Carlquist, S. 1980. Hawai'i: A Natural History. Second Edition. Pacific Tropical Botanical Garden, Lāwa'i, Kaua'i, Hawai'i.

Cassin, J. 1858. United States Exploring Expedition, during the years 1838, 1839, 1840, 1841, 1842. Under the Command of Charles Wilkes, U. S. N. mammalogy and ornithology. C. Sherman and Sons, Philadelphia 8: 1-466.

Cory, C. 1984. Pollination biology of two species of Hawaiian Lobeliaceae (*Clermontia kakeana* and *Cyanea angustifolia*) and their presumed coevolved relationship with native honeycreepers (Drepanididae). M.A. thesis, California State Univ., Fullerton, California.

Ehrendorfer, F. 1979. Reproductive biology in island plants. Pages 293-306 *in* D. Bramwell, ed. Plants and Islands. Academic Press, London.

Fancy, S. G., and C. J. Ralph. 1998. ʻIʻiwi (*Vestiaria coccinea*). Pages 1-14 *in* A. Poole and F. Gill, eds. The birds of North America, No. 327. The birds of North America, Inc., Philadelphia.

Fleischer, R. C., and C. E. McIntosh. 2001. Molecular systematics and biogeography of the Hawaiian avifauna. Stud. Avian Biol. 22: 51-60.

Fleischer, R. C., H. F. James, and S. L. Olson. 2008. Convergent evolution of Hawaiian and Australo-Pacific honeyeaters from distant songbird ancestors. Curr. Biol. 18: 1927-1931.

Gardener, M. C., and C. C. Daehler. 2006. Documenting floral visitors to rare Hawaiian plants using automated video recordings. Pac. Conserv. Biol. 12: 189–194.

Giambelluca, T. W., Q. Chen, A. G. Frazier, J. P. Price, Y.-L. Chen, P.-S. Chu, J. K. Eischeid, and D. M. Delparte. 2013. Online Rainfall Atlas of Hawaiʻi. Bull. Amer. Meteor. Soc. 94, 313-316, doi: 10.1175/BAMS-D-11-00228.1.

Givnish, T. J., K. J. Sytsma, J. F. Smith, and W. J. Hahn. 1995. Molecular evolution, adaptive radiation, and geographic speciation in *Cyanea* (Campanulaceae, Lobelioideae). Pages 288–337 *in* W. L. Wagner and V. Funk, eds. Hawaiian Biogeography: Evolution on a Hot Spot Archipelago. Smithsonian Institution Press, Washington, D. C.

Givnish, T. J., K. C. Millam, A. R. Mast, T. B. Paterson, T. J. Theim, A. L. Hipp, J. M. Henss, J. F. Smith, K. R. Wood, and K. J. Sytsma. 2009. Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). Proc. R. Soc. Lond., Ser. B: Biol. Sci. 276(1656): 407-416.

Goodwillie, C., S. Kalisz, and C. G. Eckert. 2005. The evolutionary enigma of mixed mating systems in plants: occurrence, theoretical explanations, and empirical evidence. Annu. Rev. Ecol. Evol. Syst. 36: 47–79.

Gorresen, P. M., R. J. Camp, M. H. Reynolds, B. L. Woodworth, and T. K. Pratt 2009. Status and trends of native Hawaiian songbirds. Pages 108-136 *in* T. K. Pratt, C. T. Atkinson, P. C. Banko, J. D. Jacobi, and B. L. Woodworth, eds. Conservation Biology of Hawaiian Forest Birds: implications for island avifauna. Yale University Press, New Haven.

Griffin, A. M., and Byers, D. L. 2012. Pollinator behavior differs between female and hermaphroditic plants of *Lobelia spicata*. Lam. (Campanulaceae). J. Torrey Bot. Soc. 139(2): 131-136.

Johnston, M. O. 1993. Tests of two hypotheses concerning pollen competition in a self-compatible, long-styled species (*Lobelia cardinalis*: Lobeliaceae). Am. J. Bot. 80(12): 1400-1406.

Lammers, T. G. and C. E. Freeman. 1986. Ornithophily among the Hawaiian Lobelioideae (Campanulaceae): evidence from floral nectar sugar compositions. Am. J. Bot.73: 1613–1619.

Lammers, T. G. 2007(a). Revision of *Lobelia* sect. *Galeatella* (Campanulaceae: Lobelioideae). J. Bot. Res. Inst. Texas 1(2): 789-810.

———. 2007(b). World checklist and bibliography of Campanulaceae. Royal Botanic Gardens, Kew, Surrey, United Kingdom.

———. 2009. Revision of the Endemic Hawaiian genus *Trematolobelia* (Campanulaceae: Lobelioideae). Brittonia 61(2): 126-143.

Munro, G. C. 1960. Birds of Hawaiʻi. Second Edition. Charles E. Tuttle Co., Inc., Rutland, Vermont.

Pender, R. J. 2013. Floral evolution and pollination ecology in the Hawaiian lobeliad genus, *Clermontia* (Campanulaceae). Unpublished Ph.D dissertation. Botany Department, University of Hawaiʻi at Mānoa.

Pender, R. J., C. W. Morden, and R. E. Paull. 2014. Investigating the pollination syndrome of the Hawaiian lobeliad genus *Clermontia* (Campanulaceae) using floral nectar traits. Am. J. Bot. 101(1): 1-5.

Perkins, R. C. L. 1895. Notes on some Hawaiian birds. Ibis 1895: 117-129.

———. 1901. An introduction to the study of the Drepanididae, a family of birds peculiar to the Hawaiian Islands. Ibis 8th Ser. 1: 562-585.

———. 1903. Vertebrata (Aves). Pages 365-466 *in* D. Sharp, ed. Fauna Hawaiiensis or the Zoology of the Sandwich (Hawaiian) Isles, Vol 1, Part IV. Cambridge University Press, Cambridge.

Porter, R. H., M. Durrell and H. J. Romm. 1947. The use of 2, 3, 5-Triphenyl-Tetrazoliumchloride as a measure of seed germinability. Plant Physiol. 22(2): 149-159.

Richards, L. P., and W. J. Bock. 1973. Functional anatomy and adaptive evolution of the feeding apparatus in the Hawaiian honeycreeper genus *Loxops* (Drepanididae). Ornithological Monogr. No. 15.

Rock, J. F.1919. A monographic study of the Hawaiian species of the tribe Lobelioideae, family Campanulaceae. Memoirs of the B. P. Bishop Museum 7(2): i-xvi, 1-395.

Rothschild, L. W. 1893-1900. The avifauna of Laysan and the Neighboring Islands: with a complete history to date of the birds of the Hawaiian possessions. Two volumes. R. H. Porter, London.

Speith, H. T. 1966. Hawaiian honeycreeper, *Vestiaria coccinea* (Forster), feeding on lobeliad flowers, *Clermontia arborescens* (Mann) Hillebr. Am. Nat. 100: 470-473.

Stone, B. C. 1967. A review of the endemic genera of Hawaiian plants. Bot. Rev. 33: 216-259.

van Riper, S. G. 2000. Japanese white-eye, *Zosterops japonicus* (Passeriformes: Zosteropidae). *In*: A Poole and F. Gill (eds.) *The Birds of North America*, No. 487. The Birds of North America, Inc., Philadelphia.

Wagner, W. L., D. R. Herbst, and S. H. Sohmer. 1999. Manual of the Flowering Plants of Hawai‘i. Two Volumes. University of Hawai‘i Press, Honolulu.

Warner, R. E. 1968. The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. Condor 70: 101-120.

Wilson, S. B. 1890. On some of the birds of the Sandwich Islands. Ibis ser. 6(2): 170-196.

Young, T. P. 1982. Bird visitation, seed-set, and germination rates in two species of *Lobelia* on Mount Kenya. Ecology 6: 1983-1986.