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## Odd for an Ericad: Nocturnal Pollination of *Lyonia lucida* (Ericaceae)

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**ABSTRACT.**—Studies of pollination biology are largely diurnally biased, especially in plant species whose flowers conform to diurnal pollination syndromes. Though these syndromes can be useful in generating hypotheses regarding a species' primary pollinators, they may also lead to incorrect assumptions. This study explores the relative contributions of diurnal and nocturnal pollination to fruit set in *Lyonia lucida*, an ericaceous shrub of the southeastern United States whose floral form suggests pollination by bumble bees. Floral visitation to *L. lucida* and pollen loads of visitors were quantified in a population of the species in Central Florida (U.S.A.), and the relative contributions of diurnal and nocturnal pollination tested. Mating system characteristics of *L. lucida* were also examined. Results show *L. lucida* flowers are visited mainly by nocturnal moths, who are capable of carrying large pollen loads, and nocturnal pollination is the primary driver of fruit set. In addition *L. lucida* at the study site shows severe barriers to selfing and strong pollen limitation. This is the first time a population of an ericaceous species has been shown to be pollinated primarily by nocturnal floral visitors and suggests pollination biologists should not be so quick to discount these potentially important pollinators.

### INTRODUCTION

The rapid diversification of angiosperms in the Cretaceous was a radiation *nonpareil*—in just 40 million years the group came to dominate global floras in both diversity and abundance (Wolfe, 1997; Crane and Lidgard, 1990). Accompanying divergence in physiology, growth form, and ecological attributes was a spectacular diversification in the hallmark trait of angiosperms, the flower. Interactions between plants and pollinators via the floral interface is one of the most oft-cited mechanisms to explain this floral diversity, a theory which has extensive empirical and phylogenetic support (Faegri and van der Pijl, 1979; Stebbins, 1970; van der Niet and Johnson, 2012; for review see Fenster *et al.*, 2004). Investigations of these plant-pollinator interactions have contributed much to a broad spectrum of fields, from community ecology (*e.g.*, Moeller, 2004; Palmer *et al.*, 2003) to floral evolution (*e.g.*, Fenster *et al.*, 2004; Smith *et al.*, 2008; Sun *et al.*, 2014).

The convergent evolution of some floral features across distantly related taxa has led to the concept of “pollination syndromes,” suites of floral characteristics that indicate a plant species' primary or most effective pollinator (*e.g.*, bees, birds, moths, bats, *etc.*) (Faegri and van der Pijl, 1979). These floristic characters are thought to be the result of selection for efficient attraction of and pollination by a particular functional group of pollinators (Faegri and van der Pijl, 1979; Fenster *et al.*, 2004). For example a plant species exhibiting a bat pollination syndrome might have large nocturnally accessible flowers which are strongly scented and nectar-rich (Rosas-Guerrero *et al.*, 2014; Faegri and van der Pijl, 1979). Using floral form to generate hypotheses regarding pollination ecology was most famously advanced by Darwin, who predicted in 1862 that the long-spurred *Angraecum sesquipedale* orchid would be visited by a similarly long-tongued moth, a hypothesis proven correct 130 y later (Wasserthal, 1997).

Much research has investigated the validity of pollination syndromes and how useful these floral characters actually are for predicting particular aspects of a plant's pollination ecology (see reviews in Fenster *et al.*, 2004; Johnson and Steiner, 2000; Waser *et al.*, 1996). Researchers have questioned whether a plant species' adherence to a particular syndrome indicates a high degree of specialization in plant-pollinator interactions, or whether the predictability and/or specificity of these interactions is overstated. Over the past two decades some have argued generality in interactions may be the rule and specialization the exception (*e.g.*, Waser *et al.*, 1996). But other authors have been reluctant to forgo the syndrome concept, even using these floral keys to infer plant-pollinator interactions without empirical evidence (*e.g.*, Goldblatt *et al.*, 2001; Machado and Lopes, 2004; Knapp, 2010).

Meta-analyses have shown mixed results—a global evaluation of pollination syndromes by Ollerton *et al.* (2009) found only 30% of considered species had a pollination mode consistent with their syndrome; however, a recent quantitative review by Rosas-Guerrero *et al.* (2014) showed support for the syndrome concept based on a survey of 417 plant species' most effective pollinators. Therefore, the biological reality of pollination syndromes and the extent of floral specialization remain topics of much debate. Plant species whose floral form closely matches a certain syndrome can provide important test cases to elucidate the strengths and limitations of these syndrome concepts.

The widely distributed Ericaceae are associated with two main pollination syndromes (Lutelyn, 2002). Many inferior-ovaryed Neotropical species are pollinated primarily by hummingbirds and exhibit strong signs of a bird pollination syndrome, with large red to orange flowers and long tubular corollas lacking odiferous cues. However, most ericads in temperate and subtropical latitudes, and superior-ovaryed taxa in the neotropics, are classically associated with pollination by bees (Lutelyn, 2002).

Though hundreds of studies on pollination biology within the Ericaceae have been published, one large contingent of prospective pollinators remains largely unexplored. The vast majority of pollination studies across all plant families focus on diurnal visitors, but recent work suggests we are potentially missing important visitor assemblages by ignoring nocturnal activity (Devoto *et al.*, 2011). Investigating pollination environments outside the boundaries set by precedent or syndrome has the potential to bring novel insights to our understanding of plant-pollinator interactions, and in Ericaceae we find a system well suited to this aim. Only five published studies have examined nocturnal visitors in this family, with just two experimentally testing the importance of diurnal vs. nocturnal pollination (Cutler *et al.*, 2012; Navarro *et al.*, 2008). Both of these studies found evidence of nocturnal pollination, but diurnal pollination was the main driver of fruit set.

The ericad genus *Lyonia* Nutt. shows patterns in floral morphology consistent with a bumble bee pollination syndrome, including urceolate corollas, poricidal anthers, and pendulous fragrant inflorescences (Faegri and van der Pijl, 1979; Judd, 1981; Navarro *et al.*, 2007; Willmer, 2011). Many studies have focused on bee pollination in Ericaceae, especially in regard to the economically important blueberry, *Vaccinium* spp. (*e.g.*, Wood, 1961; Aras *et al.* 1996). Though very few studies have examined pollination in *Lyonia*, the literature available points to bumble bees as primary pollinators (Lovell and Lovell, 1935; Osada *et al.*, 2003). In central Florida, U.S.A. three *Lyonia* species occur in sympatry, with *Lyonia ferruginea* Nutt. and *Lyonia fruticosa* (Michx.) G.S. Torr. flowers frequented by various Hymenoptera (Deyrup *et al.*, 2002; M. Deyrup, pers. comm.). The third species, *L. lucida* K.Koch, has been noted to rarely receive floral visits (M. Deyrup, pers. comm.) despite having large floral displays and floral characteristics classically associated with pollination by bumble bees or other bees.

Here diurnal and nocturnal pollination in *L. lucida* were explored, along with basic aspects of its reproductive biology (which has never been investigated). The study addressed five primary questions: who are the diurnal and nocturnal floral visitors of *L. lucida*? Do nocturnal visitors carry pollen loads? What is the relative importance of diurnal and nocturnal pollination to fruit set? Does *L. lucida* show signs of self-incompatibility? Does *L. lucida* show evidence of pollen limitation in central Florida?

## METHODS

### THE SPECIES

Fetterbush (*Lyonia lucida*) is a widespread shrub of the southeastern coastal plain, ranging from Virginia to Florida, with an outlying population in Cuba (Flora of North America, 1993). Commonly found in moist acidic environments, *L. lucida* grows 2.5–5 m tall with multiple stems and thick, evergreen, elliptic leaves. Flowering occurs during spring—summer, with plants producing large numbers of pendulous urceolate flowers in axillary clusters. Flower color ranges from pink to white, with corolla lengths from 5–9 mm; corolla openings are 2–5 mm wide (Fig. 1). Ten S-shaped filaments encircle the ovary at the base of the corolla, with the poricidal anthers facing inward and pressing against the columnar style, which rises to roughly 1 mm below the mouth of the corolla (Judd, 1981). The *L. lucida* flower displays many characteristics classically associated with pollination by bumble bees: pendulous fragrant blossoms with an urceolate corolla that contains a hidden nectar-secreting disc at the base of the ovary and poricidally dehiscent anthers (Judd, 1981; Faegri and van der Pijl, 1979; Proctor *et al.*, 1996; Willmer, 2011). Other ericaceous species with similar floral morphology are strongly associated with bumble bee pollination, including *Lyonia ligustrina* (L.) DC. (Lovell and Lovell, 1935), *Arctostaphylos uva-ursi* (L.) Spreng. (Haslerud, 1974), and *Pieris japonica* D. Don ex G. Don (Osada and Sugiura, 2006). Fetterbush's two congeners at the study site in central Florida (U.S.A.), *L. fruticosa* and *L. ferruginea*, are visited frequently by various Hymenoptera (Deyrup *et al.*, 2002; M. Deyrup, pers. comm.). However, researchers in central Florida have observed visitation to *L. lucida* flowers, by any potential pollinator, is extremely low (M. Deyrup and L. Riopelle, pers. comm.).

### STUDY AREA

Research was conducted during April 2013 at Archbold Biological Station (ABS), a 2101 ha reserve located at the southern end of the Lake Wales Ridge in south-central Florida (Lat: 27°11'N, Long: 81°21'W). At ABS, *L. lucida* is found most often in flatwoods, scrubby flatwoods, along the edges of seasonal ponds, and infrequently on xeric upland soils. Plants included in the study were large (>1 m tall) reproductively active individuals growing in scrubby flatwoods or at the scrubby flatwoods/flatwoods interface, in a matrix of scrub palmetto (*Sabal etonia* Swingle ex Nash), saw palmetto (*Serenoa repens* (W. Bartram) Small), and sand live oak (*Quercus geminata* Small). ABS lies within a pyrogenic ecosystem, and ABS tracts undergo controlled burns at varying intervals. Plants in this study were located in stands of varying fire histories, though none had been burned more recently than 2009.

### VISITOR OBSERVATIONS

In order to quantify floral visitation frequencies, diurnal (0700–1930 h) and nocturnal (2000–0400 h) pollinator watches were conducted in patches of *L. lucida* on 16 d during 7 April–26 April 2013, totaling 34 observation periods (631 min total; 350 min diurnal, 281 min nocturnal). Total floral visitors were counted for each observation period, then divided by the length of the observation period (in minutes) to obtain an average 'visitors per

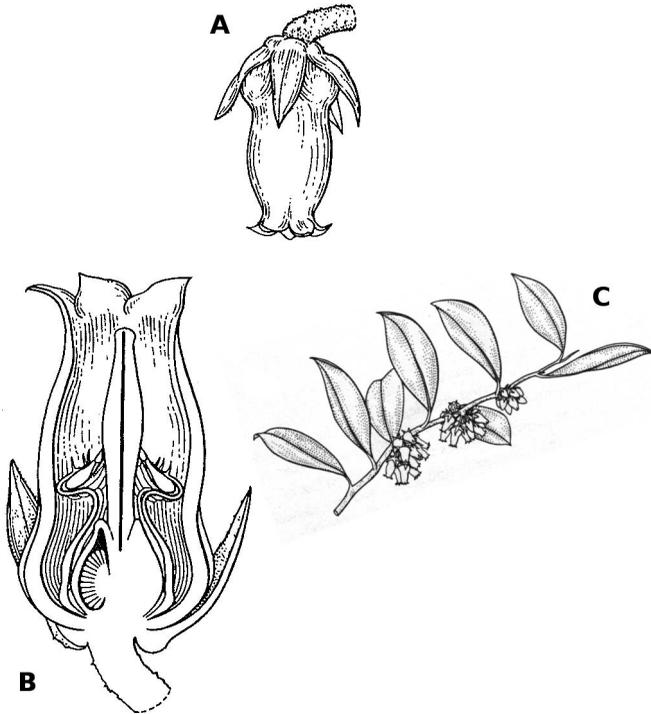


FIG. 1.—(A) *Lyonia lucida* flower; (B) longitudinal cross section of *L. lucida* flower; (C) *L. lucida* branch showing axillary clusters of flowers. Illustrations by Wendy Zomlefer, 1994. Used with permission.<sup>1</sup>

minute' for each of the 34 observations. Due to the infrequent visitation to *L. lucida*, one "patch" (5–10 plants) was monitored per watch period. Nocturnal watches were conducted using a headlamp outfitted with red LEDs.

#### VISITOR COLLECTION

To assess the potential pollinator assemblage of *L. lucida*, representative specimens of diurnal and nocturnal visitors were collected with a sweep net and identified to species. To verify nocturnal visitors carried pollen loads and therefore were potentially effective pollinators, proboscides of all nocturnal visitors collected ( $n = 22$ ) were removed and placed in 80  $\mu\text{L}$  70% EtOH. These samples were vortexed for 20 sec, then a 20  $\mu\text{L}$  subsample was removed and pipetted onto a slide. A small cube of fuschin dye (Kearns and Inouye, 1993) was melted onto the slide to stain pollen grains, which were then counted using a Nikon compound microscope. Total pollen loads for each specimen were extrapolated from this 20  $\mu\text{L}$  subsample.

#### POLLINATOR EXCLUSION EXPERIMENTS

To assess the relative importance of diurnal and nocturnal pollination, floral visitor exclusion experiments were carried out on 10 plants distributed along a ~6 km north-south

<sup>1</sup>From GUIDE TO FLOWERING PLANT FAMILIES by Wendy Zomlefer. Copyright 1994 by Wendy B. Zomlefer. Published by the University of North Carolina Press. Used by permission of the publisher. [www.uncpress.unc.edu](http://www.uncpress.unc.edu)

transect at ABS. On each plant three stems were subjected to three different treatments: control ( $n = 87$  flowers), diurnal exclusion ( $n = 118$  flowers), and nocturnal exclusion ( $n = 92$  flowers). All flowers included in the study were unopened when the experiment began. Control stems were left open to any potential pollinators. In order to exclude diurnal or nocturnal pollinators, plants were visited at sunrise and sunset ( $\pm 30$  min) to either place or remove Delnet mesh pollinator exclusion bags (DelStar Technologies, Middle Town, DE, U.S.A.); each bag covered 5–24 flowers on the treatment stem. At sunrise bags were removed from nocturnal exclusion stems and placed on diurnal exclusion stems; at sunset the process was reversed. All bags were attached with a cottonball collar surrounding the stem and secured with a plastic twist tie. At the end of April 2013 all exclusion bags were removed from stems. Flowers to be analyzed for fruit set were marked with colored thread and fruits were allowed to mature over the summer.

#### MATING SYSTEM EXPERIMENTS

The effects of selfing versus outcrossing on fruit set was examined using supplemental hand pollinations. Plants were sampled from three *L. lucida* patches (two plants per patch) arranged latitudinally across ABS; these patches also contained plants in the pollinator exclusion experiment and were  $>1$  km apart. On each plant three different stems were exposed to three treatments: a control open to any visitors ( $n = 54$  flowers), hand pollination with self pollen ( $n = 36$  flowers), and hand pollination with outcross pollen ( $n = 56$  flowers). Self pollen was obtained via sonication from flowers on the same plant while outcross pollen was obtained from *L. lucida* individuals located more than 5 m from the study individual (*L. lucida* can produce ramets extending several meters; therefore, it was important to avoid crossing among ramets of the same genet). Pollen was applied to receptive stigmas using a felt-tipped toothpick once flowers were fully opened. Hand pollinated flowers were covered in the same Delnet mesh pollinator exclusion bags used in the pollinator visitation experiments, except for the brief periods when pollen was being applied to stigmas—during this period, no visits to these flowers were observed. Each bag covered 6–25 flowers per treatment stem. All treated flowers were closed buds when initially enclosed in the mesh. To test for autonomous self-pollination, three additional stems were enclosed in mesh pollinator exclusion bags and left enclosed for the duration of the study period ( $n = 70$  flowers); these stems were all paired with a control stem (open to all floral visitors) on the same plant. At the end of April 2013, all exclusion bags were removed from stems. Flowers to be analyzed for fruit set were marked with colored thread and fruits were allowed to mature over the summer.

#### FRUIT COLLECTION

Stems were collected by a colleague in early September 2013 and shipped to the author for analysis of fruit set. Fruit set was scored for each stem as the number of fruits produced from the original number of marked flowers.

#### STATISTICAL ANALYSIS

Differences in diurnal and nocturnal visitation were analyzed with a Student's *t*-test. For the pollinator exclusion and mating system experiments, treatment effects on fruit set were fit with a generalized linear mixed effects model (including *plant* as a random factor) using the *glmer* function (family = binomial, link = logit) in the R statistical environment (R Core Development Team, 2012). If there was a significant effect of treatment, all pairwise treatment contrasts were tested with Tukey HSD tests.

## RESULTS

## VISITOR OBSERVATIONS

Nocturnal visitation was five times more frequent than diurnal visitation (average visitation: 1.93 visitors/10 min/patch and 0.4 visitors/10 min/patch, respectively) (Student's *t*-test,  $t = -3.96$ ,  $P < 0.001$ ). Other than a single butterfly visit, diurnal visitors consisted solely of one bumble bee species, *Bombus bimaculatus*. Specimen collection revealed a diverse nocturnal moth visitor assemblage, with eight moth species recorded. These included *Agrotis ipsilon*, *Feltia subterranea*, *Anicla infecta*, *Melipotis fasciolaris*, and four other unidentified Noctuidae.

## MOTH POLLEN LOADS

Pollen grains were found in tightly packed clumps on the proboscides of nocturnal visitors, who were capable of carrying large pollen loads (Figs. 2 and 3). Average pollen load size of collected moths was 617 grains ( $SD = 943$ ), with 88% of individuals carrying at least some pollen (Fig. 4). Several moth proboscides carried over 1000 pollen grains. All pollen observed was from *Lyonia* sp., though differentiating between the three *Lyonia* species at ABS was not possible using morphological characteristics.

## POLLINATOR EXCLUSION EXPERIMENTS

Binomial models revealed a highly significant effect of exclusion treatment on fruit set ( $n = 30$ , Type II Wald  $\chi^2$  test,  $P = 0.0068$ ). Tukey pairwise comparisons showed that flowers accessible only at night were as likely to set fruit as flowers open 24 h per day ( $P = 0.53$ ), but flowers only accessible diurnally were significantly less likely to set fruit than both control ( $P < 0.01$ ) and nocturnally available ( $P = 0.05$ ) flowers (Fig. 5). Nocturnally available flowers were twice as likely to set fruit than diurnally available flowers.

## MATING SYSTEM EXPERIMENTS

Binomial models revealed a highly significant effect of pollination treatment on fruit set in the mating system experiment ( $n = 22$ , Type II Wald  $\chi^2$  test,  $P < 0.001$ ). Flowers excluded from all visitors had an extremely low probability of fruit set (0.015), as did those flowers hand-pollinated with self pollen (0.026), suggesting that fetterbush is highly self-sterile and largely dependent on outcrossing for fruit set (Fig. 6). Control flowers in this experiment showed fruit set probabilities similar to controls in the visitor exclusion experiment (0.335 and 0.366, respectively), but flowers with supplemental cross pollen showed drastically higher probability of fruit set than any other treatment (0.826), suggesting high pollen limitation.

## DISCUSSION

Animal-mediated pollination is one of nature's best known and most important symbioses, with significant ecological, evolutionary and economic impacts (Kearns *et al.*, 1998). Therefore it is especially crucial to understand instances where interactions deviate from the "norm." Investigations of plant-pollinator interactions are consistently biased toward diurnal observations, likely due to overconfidence in syndrome predictions, reluctance to break from established methodology, and our inherent circadian preferences. Results from this study show that in a central Florida population of a common ericad, nocturnal pollination is the primary driver of fruit set, despite the species' floral morphology suggesting a dominance of bee pollination. Only five other published studies have looked for Ericaceae floral visitors after dark (Cutler *et al.*, 2012; Devoto *et al.*, 2011;

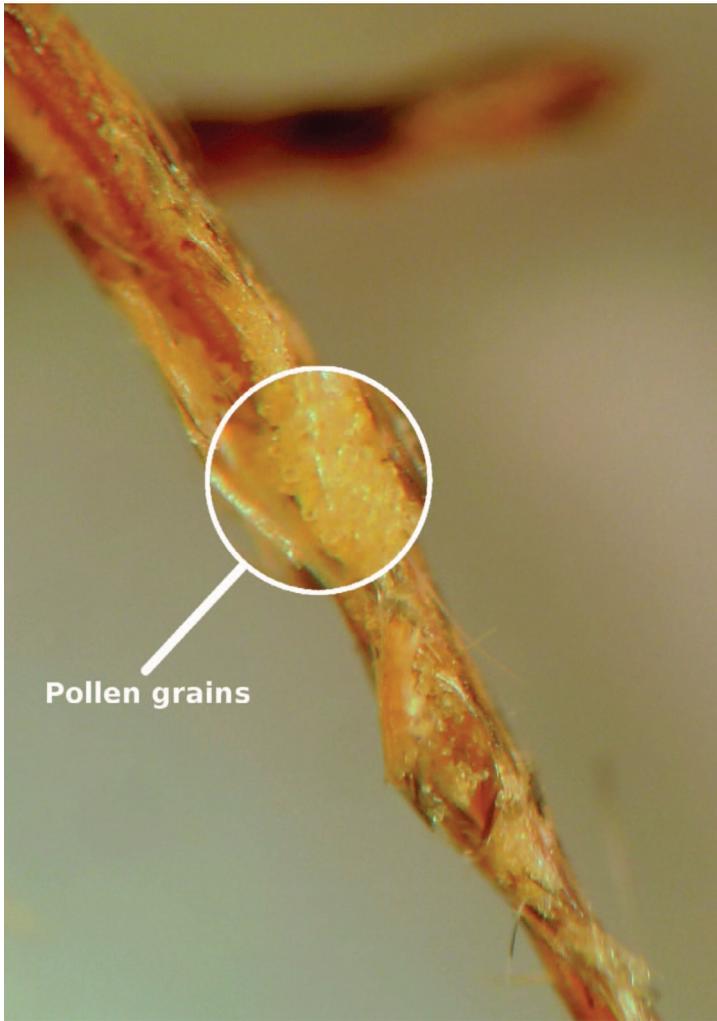


FIG. 2.—*Lyonia* pollen load on extended moth proboscis, with enlarged inset showing clumped pollen grains

Manning and Cutler, 2013; Navarro, 1999; Van der Niet *et al.*, 2014) and this is the first to experimentally show nocturnal visitors as the primary pollinator of an ericaceous species.

This is also the first study to examine the reproductive biology of *L. lucida*, a species that at ABS seems to experience strong pollen limitation and severe barriers to selfing, a combination that makes it particularly vulnerable to habitat change (Aguilar *et al.*, 2006; Young *et al.*, 2012) and can decrease population viability (Young *et al.*, 2012). The potential for these effects is especially high in central Florida, an area that has experienced high rates of habitat destruction in recent decades (Turner *et al.*, 2006; Weekley *et al.*, 2008).

But why has fetterbush adopted this unique pollination mode, and what mechanisms are involved in its maintenance? Though *L. lucida* does exhibit strong symptoms of melittophily, it



FIG. 3.—*Lyonia* pollen load on retracted moth proboscis, with enlarged inset showing clumped pollen grains

is important to note differences in floral characters between it and its two sympatric congeners at ABS. Most notable is the difference in corolla length—while *L. lucida* corollas can range from 5–9 mm long, its congeners' flowers are noticeably shorter, with *L. ferruginea* flowers ranging from 2–3 mm and *L. fruticosa* from 4–5 mm in length (Flora of North America, 1993). At ABS, *L. lucida* corollas average 8.5 mm (SD = 0.5) in length (J. Benning, pers. obs.). This difference in floral morphology is accompanied by an ecological divergence between *L. lucida* and its congeners. The former, while able to subsist in drier scrubby flatwoods, shows preference for more mesic sites (e.g., edges of flatwoods and ponds), while *L. fruticosa* and *L. ferruginea* are more common in xeric habitats at ABS (Weekley *et al.*, 2006; Flora of North America, 1993). These three sympatric congeners flower concurrently, a situation which can lead to pollinator competition and/or increased heterospecific pollen deposition and in turn selection for reproductive character displacement via divergence in floral characteristics (Waser, 1983). One other congener in Florida, *Lyonia mariana* D. Don, shows a range of corolla lengths similar to *L. lucida*, though no studies have examined its pollination ecology.

Theoretical work has shown that long corollas may evolve as a result of competition for pollinator resources and as a means to increase conspecific pollen transfer (Rodríguez-Gironés and Santamaría, 2007). By excluding visitors with short proboscides via its extended corolla, fetterbush may be able to specialize on relatively long-tongued moths, increasing

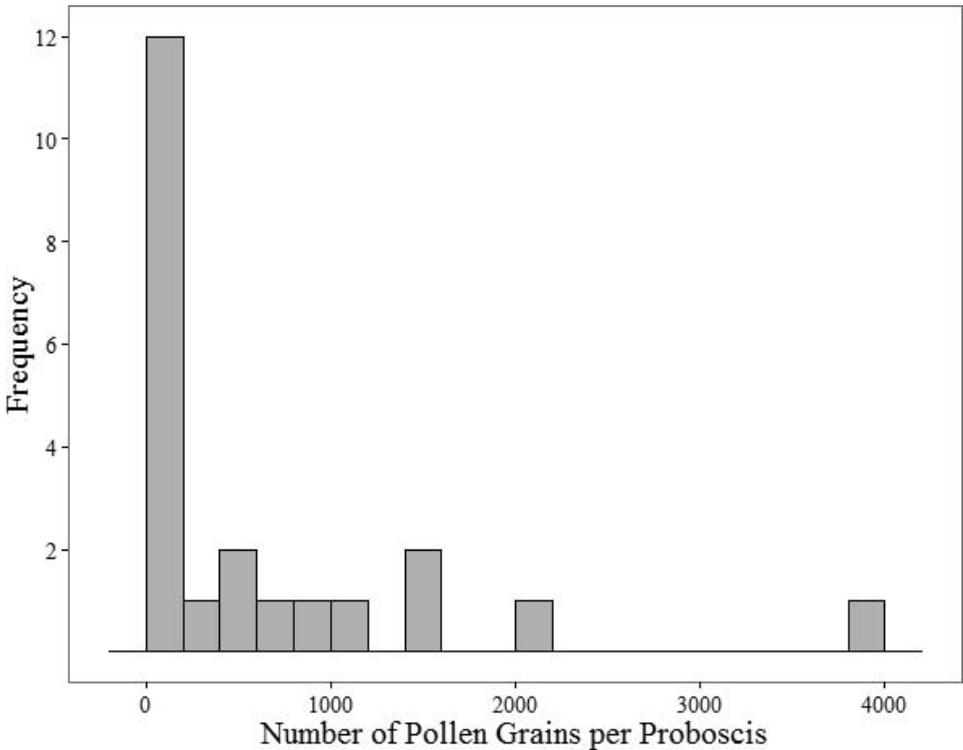


FIG. 4.—Histogram of pollen loads found on proboscides of moths visiting *L. lucida*

conspecific pollen transport and limiting deposition of heterospecific pollen by more generalist bees. It is of note the one bumble bee visitor that was found on *L. lucida*, *Bombus bimaculatus*, is relatively long-tongued. In investigating pollination of another ericad in the southeastern U.S., Dorr (1981) found that *B. bimaculatus* had a mean proboscis length of 7.4 mm, ~25% longer than *Bombus impatiens*, the most common bumble bee species at ABS and a frequent visitor of *L. ferruginea* and *L. fruticosa* (Deyrup *et al.*, 2002). As this is the first record of *B. bimaculatus* at ABS, this bee may be relatively rare in these fetterbush populations and therefore an inconsistent or unreliable pollinator.

At this point many of these details are anecdotal, but spur an interesting set of questions for future work: does *L. lucida*'s extended corolla result in exclusion of short-tongued visitors and/or decreased heterospecific pollen transfer? In terms of pollen deposition, how efficient are moths as pollinators of fetterbush? Are there fitness costs to hybridization between *L. lucida* and its congeners? Do floral traits and pollination ecology differ in *L. lucida* populations without congeners? Because this is the first in-depth investigation of *L. lucida*'s pollination ecology, nothing can be said about whether these interactions vary across the species' range. However, having such a wide variation in corolla length and a relatively broad distribution makes this species a prime system to study geographic variation in plant-pollinator-community interactions and its relationship with floral form.

Many Neotropical Ericaceae are pollinated primarily by hummingbirds, and some researchers suggest that a transition from bee-to-bird pollination might be a driver of

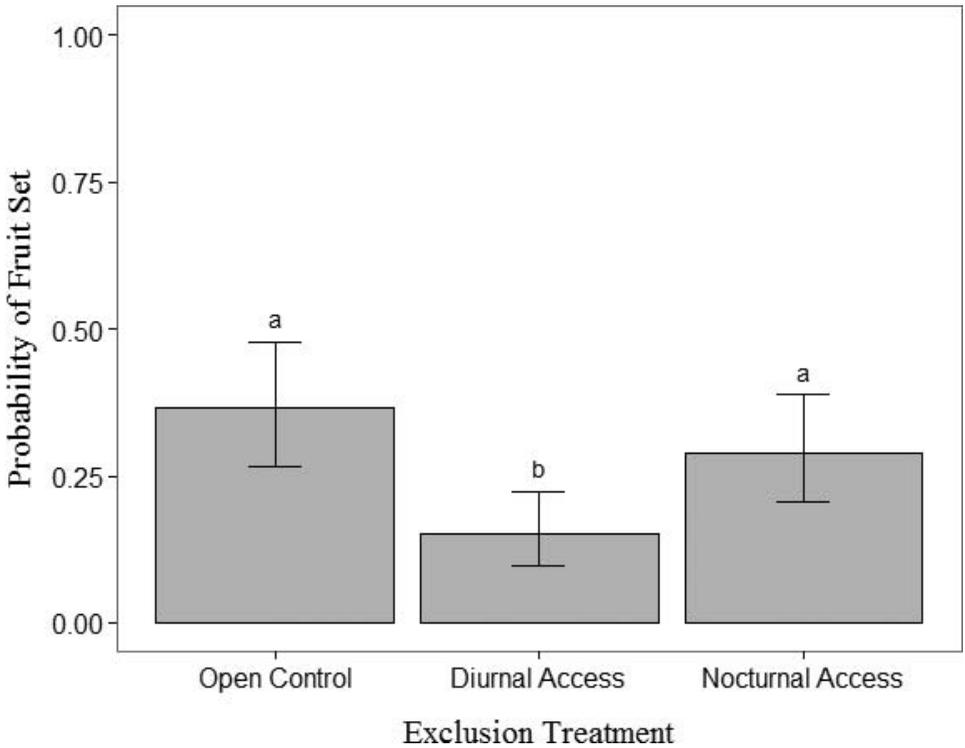


FIG. 5.—Probability of fruit set per exclusion treatments, based on GLMM. “Open Control” flowers ( $n = 87$ ) were open to visitors 24 hours/day, “Diurnal Access” flowers ( $n = 92$ ) were only accessible from sunrise to sunset, and “Nocturnal Access” flowers ( $n = 118$ ) were only accessible from sunset to sunrise. Bars are standard errors back-transformed from logit transformations. Different letters above bars indicate significant differences between treatments at  $P \leq 0.05$

diversification in this family (Luteyn, 2002). What we may be seeing in *L. lucida* at ABS is evidence of a bee-to-moth transition, which has been well documented in *Aquilegia* L. (Whittall and Hodges, 2007) and *Ruellia* L. (Tripp and Manos, 2008). In the Cape Floristic Region of South Africa, researchers recently found dominant pollinators varied with corolla length in “pollination ecotypes” of *Erica plukenetii* P.J.Bergius, with long corolla populations primarily visited by sunbirds and (relatively) short corolla populations frequented mostly by diurnal and nocturnal moths (Van der Niet *et al.*, 2014). Although the contribution of diurnal vs. nocturnal pollination to fruit set is unclear in *E. plukenetii*, these observations suggest that moth pollination may be important in other ericads and is potentially an overlooked mode of reproduction across the family.

There are instances where pollination syndromes are very accurate in predicting primary pollinators and instances, such as this one, where they seem to fall short. We must remember the floral forms we see today are the culmination of many generations of historical selection, and pollination environments have the capacity to change much more rapidly than a species’ floral characteristics, in most cases. In some systems contemporary pollinators may be exerting selective pressures on floral forms that are different from historical selective pressures, leading to a potential mismatch between floral syndrome and

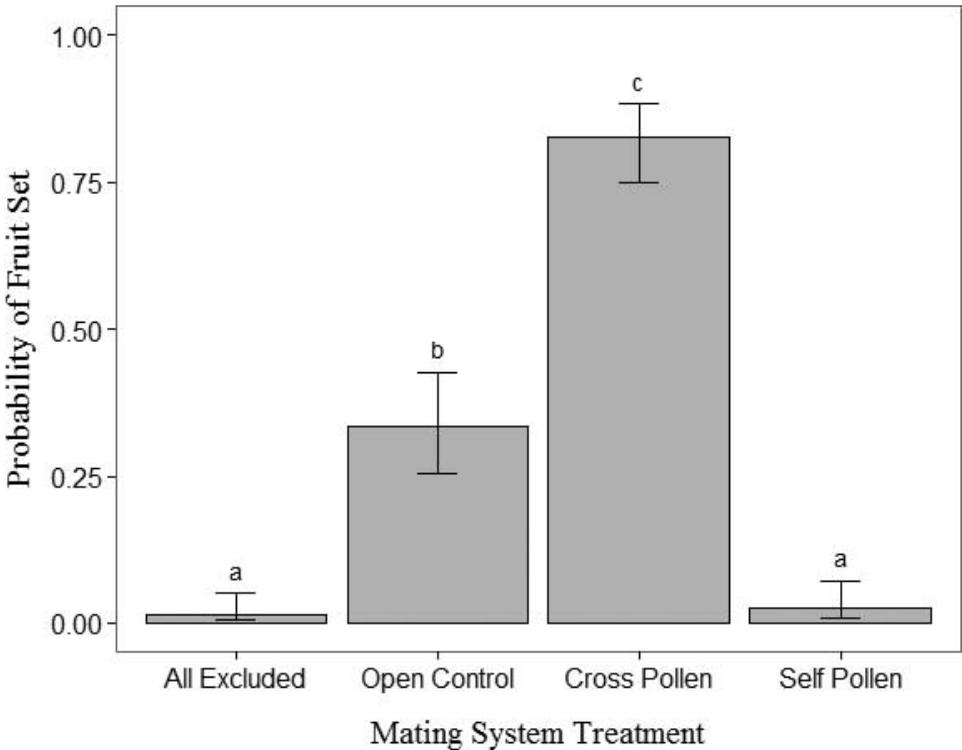


FIG. 6.—Probability of fruit set per mating system treatments, based on GLMM. “All Excluded” flowers ( $n = 70$ ) were bagged 24 hours/day, “Open Control” flowers ( $n = 54$ ) were open to visitors 24 hours/day, “Cross Pollen” flowers ( $n = 56$ ) were bagged and hand pollinated with outcross pollen, “Self Pollen” flowers ( $n = 36$ ) were bagged and hand pollinated with self pollen. Bars are standard errors back-transformed from logit transformations. Different letters above bars indicate significant differences between treatments at  $P \leq 0.05$ .

current pollinator assemblages (*e.g.*, Li and Huang, 2009). There is also evidence that secondary pollinators of a species often correspond to ancestral pollinators (Rosas-Guerrero *et al.*, 2014), a pattern that seems probable in *L. lucida* given the dominance of bee pollination in other temperate members of the genus and the absence of evidence (in any taxa) for transitions from moth to bee pollination.

The floral syndrome concept can generate informed hypotheses to test but should not be relied upon as an accurate predictor of pollination mode without empirical evidence. Cases where pollination syndromes do *not* predict the primary pollinator can give us even greater insight into the mechanisms and patterns of coevolution in plant-pollinator relationships, and we should be careful not to dismiss potential floral visitors too quickly—there could be many surprises awaiting pollination biologists after dark.

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