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Display Size Preferences and Foraging Habits of High Andean Butterflies Pollinating *Chaetanthera lycopodioides* (Asteraceae) in the Subnival of the Central Chilean Andes

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Abstract

In our study, we asked whether butterflies visiting *Chaetanthera lycopodioides* (Asteraceae) in the subnival at 3450 m a.s.l. in the central Andes prefer larger floral displays. To answer this question, we compared the population distribution of display sizes with the distribution of visited display sizes at two sites. Six high elevation butterflies: *Faunula leucoglene* (Satyridae) (the dominant species), *Hylephila* sp. (Hesperiidae), *Phulia nymphula* (Pieridae), *Vanessa terpsichore* (Nymphalidae), *Tatochila mercedis* (Nymphalidae), and *Yramea modesta* (Nymphalidae) were reported as visitors. Butterflies tended to discriminate against plants with a single open head, preferring larger display sizes at both sites. Butterflies visited few plants per bout (mean: 3.1–4.5) and probed increasingly smaller proportions of the open heads per plant with increasing display size (overall mean: 45.8–48.4%). Results suggest that high elevation butterflies tend to prefer larger display sizes over smaller ones, but final choices are conditioned by the relative abundance of each display size in a population. Although previous studies show that butterflies prefer larger artificial individual flowers over smaller ones, our work appears to constitute the first report of butterfly preference for larger floral displays in any plant species or ecosystem.

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Introduction

Pollinator preference for larger floral displays has been demonstrated on numerous occasions (Ohara and Higashi, 1994; Ohashi and Yahara, 1998, 1999; Ishii and Sakai, 2001; Elle and Carney, 2003; Mitchell et al., 2004; Harder et al., 2004; Grindeland et al., 2005; Kudo and Harder, 2005), and increased display size has been interpreted as a selective response on the part of plants for capturing pollinator visits. However, to date, most studies demonstrating preference for larger display sizes pertain to bee species, with a limited number of studies on flies and hummingbirds (Ohashi and Yahara, 2001). In particular, it remains unknown whether lepidopterans prefer larger displays when confronted with a variety of floral display sizes. One early experimental study at the individual flower level has shown that butterflies prefer larger individual artificial flowers over smaller artificial flowers when given a choice (Ilse, 1932), such that it would not be surprising that larger display sizes might also be preferred by this group of pollinators. Nevertheless, Kelber (1997) showed that hawkmoths preferred individual flowers of intermediate size.

Butterflies are important flower visitors for plant life at the highest elevations (i.e., in many alpine areas) (Arroyo et al., 1982). Yet, present knowledge of floral evolution in the alpine mostly comes from bee pollination studies (Galen and Newport, 1987; Galen, 1996). Along the altitudinal gradient, butterflies tend to replace bees at the higher elevations, or become relatively more common in relation to bees than at lower elevations, on account of their lower energy requirements and their ability to undergo passive thermoregulation (Arroyo et al., 1982). Butterflies have been questioned by some authors with regard to their efficiency as pollinators, on the grounds of limited pollen transport (e.g., Wiklund et al., 1979). However, this claim does not apply to all cases of butterfly pollination (e.g., Murphy 1984; Herrera, 1987). Moreover, several authors have pointed out that in traveling large distances (Waser, 1982; Herrera, 1987; Goulson et al., 1997), butterflies will tend to promote high levels of outcrossing. Given the importance of butterflies as visitors to flowers at the highest elevations, knowledge of whether butterflies prefer larger floral displays is critical for formulating hypotheses about floral evolution in high elevation floras and for understanding floral evolution in butterfly-pollinated plants in general. Large display sizes can be expected to emit stronger scents, and thus provide multiple cues (visual and olfactory) for attracting pollinators. Butterflies are characterized as having excellent long-range vision and an exceptionally wide visual field (Merry et al., 2006), strong color constancy (Kinoshita and Arikawa, 2000; Weiss and Papaj, 2003), and well-developed olfactory capacity (Andersson, 2003). Because larger floral displays will usually signify a high local concentration of floral resources, butterflies, like bees and other pollinator groups (Ohashi and Yahara, 2001), can also be expected to prefer larger display sizes when given a choice. However, this behavioral tendency, resulting in greater efficiency in nectar collection, might be even more marked in butterflies because they divide their time between nectaring and other activities such as searching for mates and defending territories (Goulson et al., 1997).

In our research, we asked whether subnival butterflies pollinating *Chaetanthera lycopodioides* (Asteraceae), an abundant plant species between 3200 and 3600 m a.s.l. in the central Chilean Andes, preferentially visit larger floral displays. We also determined whether butterflies visit all of the open capitula head on

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a plant, taking advantage of all available floral resources offered by the plant. Studies focusing on pollinator visitation and display size preferences usually rely on comparisons of pollination visitation rates in artificial floral populations (e.g., Elle and Carney, 2003; Biernaskie and Cartar, 2004; Karron et al., 2004). Here we adopt an alternative approach in which we compare the frequency distribution of display sizes visited by pollinators with the frequency distribution of display sizes found in large, unmanipulated populations.

Study Species and Methods

Chaetanthera lycopodioides is a low-growing (3–4 cm tall), loosely branched, caespitose perennial herb endemic to the high Andes of central Chile and adjacent Argentina. Plants are characterized by showy sessile capitula (~ 16 mm diameter) bearing white, female-sterile ray florets tinged red on the underside and yellow disc florets, which strongly contrast with the tightly adpressed brownish-green foliage. *Chaetanthera lycopodioides* has been reported to be pollinated by butterflies (Arroyo et al., 1982). At peak flowering, population display sizes represent approximately 40% (one head open) to 80% (six or more head open) of a plant's full number of capitula (M. T. K. Arroyo, unpublished data). Although genetically self-compatible (M. T. K. Arroyo, unpublished data), protandry at the level of the capitulum determines that *C. lycopodioides* requires external pollinators for full achene set.

Butterfly visitation with respect to display size and number of open heads per plant was investigated at peak flowering at two subnival sites located at 3450 m in the Cerro Tres Puntas area, La Parva-Valle Nevado ski complex area, Andes of central Chile, lat 33°S. Above 3000 m a.s.l. summer days tend to be sunny in the morning and cloudy as of the early mid-afternoon (Arroyo et al., 1981). Mean annual temperature is 1.2°C at 3500 m a.s.l. (Cavieres et al., 2000). At both sites *C. lycopodioides* was very abundant, continuously distributed, and the dominant species in the vegetation (~ 90% of total plant cover), with no other showy species present in the area. The SE site was located on the upper east-southeastern side of a small dividing ridge, while the SW site was located on the southwestern side of the same ridge some 90 m away. Although the two sites are quite close, the SW side of the ridge tends to be wetter and supports higher plant cover. We chose to work at two sites in order to ascertain the generality of any patterns found.

At each site an observation plot measuring 8 m × 20 m (= 160 m^2) was marked off. Plot size followed the requirement that one be able to register long visitation sequences and obtain reliable data on display size frequencies in the population. Plants of *C. lycopodioides* occurring with a linear distance of 5 m from each of the four borders of the plots were weeded away so as to minimize carryover search images obtained outside of the patches.

Detailed observations of butterflies entering the plots (hereafter, bouts) were made by two or three observers working simultaneously over three contiguous sunny days per site (a total of six days of observation) during the period 10–19 February 2005. For as many separate butterfly bouts as we could handle (estimated at >95%), we recorded the identification of the butterfly, the display size of each plant (expressed as number of open heads) for the sequence of plants the butterfly visited in the plot on the particular bout, along with the number of open heads visited on the particular plant. Non-informative bouts, where the butterflies entered the plots but failed to make visits, were also recorded. Bouts were registered continuously from the time the first butterflies appeared (10:00–10:30 hrs) to the time they disappeared (usually 16:00–16:30 hrs), except on the third day of observations on SW when clouds appeared early in the afternoon and activity abruptly ceased. Butterfly behavior was further investigated by assessing the length of the visitation sequences and by determining the percentage of open heads visited per display size.

To establish the population distribution of display sizes, we surveyed the entire plots around midday on each observation day, scoring all plants with open heads and the number of open heads on each scored plant. Finally, as complementary information, records of air temperature were made at 5, 50, and 150 cm above ground level at 30-minute intervals.

Data Analysis

Over the three days of observation at each site, the total number of plants bearing open heads in the plots showed some variation because new heads were opening on some plants and old heads were closing on others. For statistical purposes we recognized five display sizes: plants with one, two, three, four, or five or more open heads. The frequency distribution of display sizes was indistinguishable over the three days at each site (SE: $G = 4.18$, d.f. = 8, $p > 0.05$; SW: $G = 7.01$, d.f. = 8, $p > 0.05$). This allowed us to pool the visitation data for the three days at each site. To detect display size preferences, the display size distribution of plants visited by the butterflies was compared with the population display size distribution using the G-test, where the expected frequencies for the visited plants were calculated from the population display size frequencies, reflecting the null hypothesis of no preference for larger-sized displays. In order to eliminate pseudo-replication in the comparisons of display size distributions, a single plant visited was randomly selected from the sequence of plants visited on an individual bout using a standard randomization procedure (http://www.random.org/nform.html). This procedure reduced the number of data points from 578 to 187 on SE and from 1101 to 245 on SW. We generated the population display size distribution from the average number for each display size over the three sampling days in each population. In order to visualize differences in the distribution of display sizes in the visited plants and total population, the frequency of each display size for the full sets of visited plants was subtracted from the frequency of the corresponding display size in the population.

Results

During the six sampling days the skies were virtually cloudless, except for the afternoon of day three in SW. Temperature in the shade at 10 cm a.g.l. bordered on 19–20°C, at 50 cm a.g.l. it was 14–16°C, and at 150 cm a.g.l. the temperature was 13–14°C. The mornings were totally calm until around 11:00; thereafter light to strong winds characterized both sites until around 15:30.

Display size varied considerably, from one to 13 open capitula (Fig. 1), with larger displays in the denser and more productive SW site. In both populations, more plants had one open head than any other number, with few plants displaying five or more heads. Intermediate display sizes (two to four heads open per plant) constituted around 39% of plants at the SE site and 51% of the SW sites.

Among the 904 butterfly bouts observed, a total of 432 were informative, giving 1589 plant and 1959 capitulum visits, respectively. The proportion of informative bouts was significantly

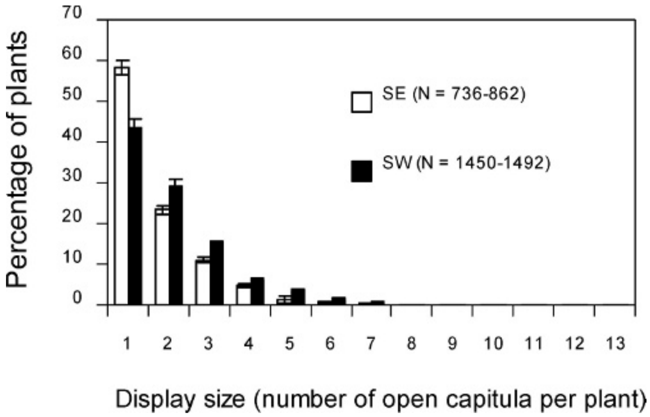

FIGURE 1. Display size distribution in *Chaetanthera lycopodioides* in SE and SW, 3450 m a.s.l. Vertical bars = 2 SE for the three sampling days. See Table 1 for number of plants with open heads at each site.

higher on the denser SW site (54.1%) as compared with SE (41.5%) (G_{adj} = 7.217, d.f. = 1, $p < 0.01$). The dominant visiting butterfly was: *Faunula leucoglene* (Satyridae) (71–81% of bouts). Other species recorded were *Hylephila* sp. (Hesperiidae), *Phulia nymphula* (Pieridae), *Tatochila mercedis* (Nymphalidae), *Vanessa terpsichore* (Nymphalidae), and *Yramea modesta* (Nymphalidae). With the exception of *Vanessa terpsichore*, an occasional visitor, which was recorded on one occasion to visit an outstanding 55 plants in a single bout in SW, the number of plant visits made by a given butterfly species was proportional to its relative bout abundance (Fig. 2). For non-informative bouts, the butterflies flew over the sampling areas without visiting *C. lycopodioides* heads or any other plant species in the patches. Visits by Dipterans were so rare that we did not even consider quantifying them, and neither were they the object of study.

The visited display size distribution was significantly different from the population display size distribution at both sites (SE: G = 14.41, d.f. = 4, $p < 0.01$; SW: G = 17.53, d.f. = 4, $p < 0.01$), there being a consistent trend in both populations for butterflies to discriminate strongly against the displays with one head in favor of larger-sized displays (Fig. 3). However, as the display sizes reached the exceptionally large sizes (> 5 heads) there was not evidence for exaggerated levels of visitation (Fig. 3); however, numbers for this display size are so small that it is difficult to make any firm statements.

The number of plants visited per bout was exceedingly low given the literally hundreds of plants in the dense sampling areas, and significantly larger on the denser SW site (Table 1; Fig. 4). On average, fewer than half of the open heads per plant were probed (Table 1), with a notable decrease with increasing display size (Fig. 5).

Discussion

Butterflies visiting natural populations of *C. lycopodioides* at 3450 m a.s.l. in the subnival discriminated against the smallest floral displays. The fact that the same trend occurred in two separate populations on opposite-facing slopes suggests that the tendency for butterflies to prefer larger displays is a generalized trend. However, the relationship is not a simple one. The very large display sizes possibly did not receive exaggerated numbers of visits because of their lower frequencies in populations of *C. lycopodioides*. Classical optimal foraging theory (Stephens and Krebs, 1986) predicts that larger flowers (or displays) should be exploited once encountered, but if their relative abundance is very low, or if their exploitation signifies excessive costs (energetic cost or predation risk, among others), then pollinators should prefer to exploit second-class flowers. Significantly, in this context, most studies considering pollinator preference and display size rely on experiments where different display sizes are offered to pollinators in equal frequencies and densities. Our results suggest that offering various display sizes in their natural frequencies could alter the finer conclusions in such experimental studies. Of course, other potential pitfalls arise when using un-manipulated natural populations. For example, it has been shown that pollinators prefer taller plants (Donnelly et al., 1998). If taller plants naturally tend to have larger inflorescences (and displays), the relationship with display size could be spurious. This last situation, however, is unlikely to be the case in *Chaetanthera lycopodioides*, where the prostrate caespitose habit determines that plant height shows little variation with plant and display size.

Whether the ultimate cue determining the display size preferences of *Chaetanthera lycopodioides* butterfly pollinators is visual or olfactory remains to be seen. Butterflies use visual cues to locate floral resources from a distance, and a combination of visual and olfactory cues at short ranges (Andersson, 2003; Honda et al., 2004). However, one recent experimental study shows that even at short ranges visual cues (e.g., color) can be more important than scent (Ômura and Honda, 2005). These various behavioral studies suggest that visual cues are likely to be relevant, at least when a butterfly initially approaches a plant from a distance. However, what is visually perceived by a pollinator is likely to change with increasing proximity to the plant. At a large distance,

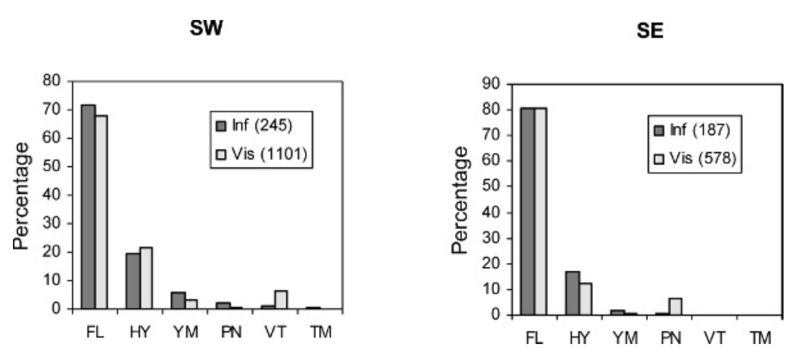

FIGURE 2. Percentage of the informative bouts (Inf) and percentage of total plant visits (Vis) made by each of the six species of butterflies visiting *Chaetanthera lycopodioides* in SE and SW, 3450 m a.s.l., central Chilean Andes. FL: *Faunula leucoglene* (Satyridae); HY: *Hylephila* sp. (Hesperiidae); YM: *Yramea modesta* (Nymphalidae); PN: *Phulia nymphula* (Pieridae); VT: *Vanessa terpsichore* (Nymphalidae); TM: *Tatochila mercedis* (Nymphalidae).

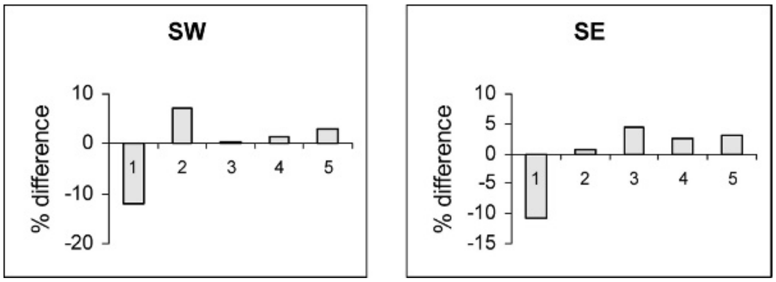

FIGURE 3. Percent difference in the frequency of each display size visited in *Chaetanthera lycopodioides* in SE and SW, 3450 m a.s.l., with respect to the frequency of those display sizes at the population level. Negative percentage values indicate display sizes that are visited at lower frequencies in relation to their respective contributions in the populations, while positive values indicate display sizes that received proportionately more visits than expected from their frequencies in the populations. One of the plants visited in the sequence of plants visited in each butterfly bout was randomly selected, giving a final sample size of $N = 187$ on SE and 245 on SW. Population sample sizes are given in Table 1.

overall display size and color are likely to be most important. However, at close range, the size of the individual flower in a display might be more important. The preference by hawkmoths for intermediate-sized individual flowers is thought to correspond to a need to perceive an image size that allows the animal to stabilize its position in space when hovering (Kelber, 1997). Individual flower size and inflorescence size tend to be seen as two sides of the same coin by pollination biologists, but this will not necessarily be the case (cf. Harder et al., 2004).

Though the butterflies visiting *C. lycopodioides* selected larger displays, counterintuitively, with respect to the expectations of optimal foraging, they avoided many of the open heads on a plant, moving quickly to the next plant. Moreover, with a few notable exceptions, there was a clear tendency for the butterflies to visit very few plants in the plots per bout (< 5). The decreasing proportion of heads probed per plant with increasing display size has been previously reported in other pollinator groups (Klinkhamer et al., 1989; Iwasa et el., 1995; Ohashi and Yahara, 2001, 2002) and has been related to the risk of a pollinator spending time on flowers that have already been handled. The proportional drop-off in butterfly-pollinated *C. lycopodioides*, however, seems to be greater than reported for bee-pollinated species. This trend could simply reflect high elevation environmental conditions as they affect pollinator behavior. In high elevations, foraging is strongly constrained by low temperatures (Arroyo et al., 1985; Bergman et al., 1996; Totland and Schulte-Herbrüggen, 2003), limiting the amount of time a pollinator can engage in active flight or foraging before resorting to passive thermoregulation. The outstanding weather conditions over the study period, however, make it unlikely that the short butterfly visits were conditioned by temperature conditions. Heads of *C. lycopodioides* are found at about 2–5 cm a.g.l., while butterflies, when foraging, tend to fly between plants at about 10–30 cm a.g.l. Temperatures at the height of butterfly flight during the study period, according to the measurements taken, were somewhere in the range of 13–14°C (50 cm a.g.l.) and 18–20°C (150 cm a.g.l.), which is not particularly cold.

Alternatively, butterflies might be coaxed into visiting the very attractive plants of *C. lycopodioides* using visual signals from a distance but fail to remain on the same plant once they are able to assess the quality of the floral resources in the first head(s) probed. Measurements of nectar are unavailable in *C. lycopodioides*, but amounts are so small as to be imperceptible to the human eye. Due to strong intra-head protandry, self-compatible *C. lycopodioides* requires pollinator visitors to obtain a full seed set. However, some intra-capitulum geitonogamy and considerable inter-capitulum geitonogamy will occur on a plant with more than one open head (cf. Galloway et al., 2002; Karron et al., 2004). Combining attractive displays with low amounts of floral resources would tend to promote outcrossing by discouraging inter-capitulum geitonogamy. Harder and Barrett (1995) have suggested that traditional interpretations of floral design and display need to be broadened to recognize their role in reducing the effect of geitonogamous pollen transfer.

Another relevant factor in *Chaetanthera lycopodioides* concerns the fact that butterflies intersperse nectaring with other activities, such as searching for mates and defending territories (Goulson et al., 1997). Over altitudinal gradients, butterflies tend to emerge later in the season and have shorter flight periods at the higher altitudes (Gutíerrez and Menéndez, 1998), such that the

TABLE 1

Comparison of *Chaetanthera lycopodioides* in SW and SE, 3540 m, central Chilean Andes.

Site	Number of plants with open capitula per day (mean, range)	Population display size (mean ± 2SE, range)	Display size of plants visited (mean ± 2SE, range)	Number of plants visited per bout (mean ± 2SE, range)	% of open heads per plant visited (mean ± 2SE, range)
SE	785.3 (736–862)	1.71 ± 0.08 (1–13)	1.99 ± 0.12 (1–13)	3.09 ± 0.45 (1–55)	45.78 ± 2.35 (50–100)
SW	1444.0 (1450–1492)	2.05 ± 0.07 (1–11)	2.28 ± 0.08 (1–10)	4.49 ± 0.66 (1–18)	48.43 ± 1.59 (50–100)

Mann-Whitney U test site comparisons. Population display size: $Z = 6.824$, $p < 0.0001$. Visited display size: $Z = 5.907$, $p < 0.001$. Number of plants visited per bout: $Z = 3.870$, $p < 0.0001$. Percentage of open heads per plant visited: $Z = 1.915$, $p > 0.05$.

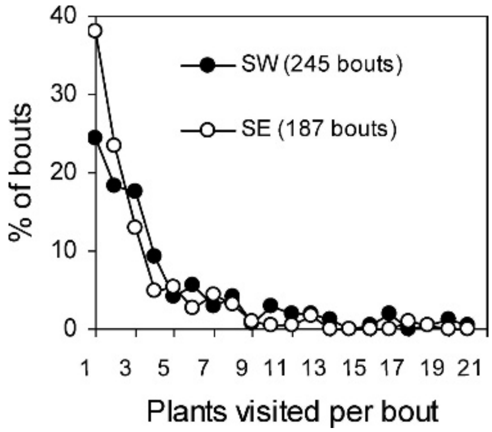

FIGURE 4. Number of plants visited per bout by butterflies in SE and SW. Bouts where more than 20 plants were visited have been grouped into a single category. Lines have been used to facilitate distinguishing the tendencies in the two sites.

aforementioned tasks must necessarily be completed over a relatively shorter period of time. On numerous occasions, we witnessed intense social interactions between butterflies, which led to the abandonment of foraging. Indeed, for about half of the bouts, the butterflies flew completely over the plots (presumably searching for mates), failing to make any visits at all. Such behavioral patterns and strong social interactions make the interpretation of butterfly foraging patterns (and their implications for floral morphology) more complex than in well-studied bee pollination systems.

Finally, the showiness of alpine plants has long drawn the attention of alpine ecologists (cf. Körner, 1999). Using allometric models, Fabbro and Körner (2004) demonstrated that although individual flowers of European alpine species are not significantly larger than those of lowland species, proportionately more of an alpine plant's resources are invested in flowers in relation to vegetative components. In addition, more of a plant's flowers remain open simultaneously, resulting in comparatively large displays. These authors suggested that the relatively higher investment in flowers together with longer-lived flowers in alpine species might be the result of strong selection favouring outcrossing under pollinator-impoverished conditions in the alpine.

Here we have documented that butterflies discriminate against the smallest floral displays. All other things being equal, butterflies would therefore tend to favour population variants that allocate relatively more of their resources to the production of flowers and larger displays. This validates a critical supposition underlying Fabbro and Körner's (2004) explanation for altitudinal changes in resource allocation in an important group of high elevation pollinators. Future ecological studies in butterfly plants might focus on the relative contribution of individual flower size versus flower number as they affect total display, and aim to determine the limits at which increases in individual flower size and inflorescence size make a difference to butterflies.

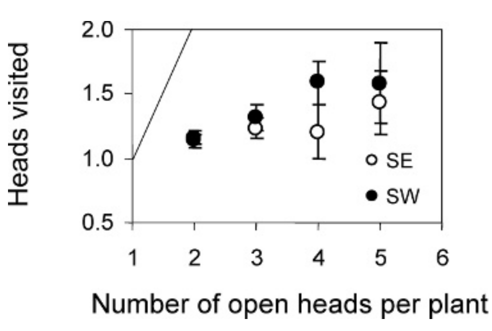

FIGURE 5. Mean number of open heads visited in relation to total heads open per plant in *Chaetanthera lycopodioides* in SE and SW, 3450 m a.s.l. Vertical bars = 2 SE of the mean for three days sampling. The line on the graph represents 100% of heads visited per plant (slope = 1).

Acknowledgments

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