Evolutionary Ecology Research, 2006, **8**: 1461–1474

Signal selection in a desert lily, *Pancratium sickenbergeri*

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ABSTRACT

Hypothesis: The optimum height of an inflorescence is expected to be the result of costs and benefits for the plant, where the benefit is pollination and the costs are herbivory and allometric growth. Thus, plants with more resources will have taller flower stalks, will provide a greater reward to pollinators, and will be preferred by pollinators. However, in populations subject to stronger herbivory, mean stalk height will be shorter.

Organism: We studied populations of a hysteranthous and tall-stalked geophyte, the Negev desert lily (*Pancratium sickenbergeri*), subject to varying levels of herbivory by dorcas gazelles (*Gazella dorcas*).

Field site: Sandy habitats in Makhtesh Katan and Makhtesh Ramon, in the Negev Desert, Israel.

Methods: We measured the survival and frequency distribution of floral stalk height, bulb size and condition (by artificially simulating bulb herbivory), pollinator preference, rewards for the pollinators (pollen grains per plant and the energetic value of the nectar per flower), and fruit and seed production. We then compared stalk height between populations and correlated stalk height, pollen and nectar, and seed production.

Results: Lilies in populations with high herbivory produced shorter inflorescences than in populations with low herbivory. The condition of the bulb affected stalk production, but not its height or seed production. The pollinator preference results were inconclusive. Taller inflorescences produced more rewards for pollinators. We observed variability in fruit and seed production due to the size of the flower stalk and this variability differed among the populations with different levels of herbivory.

Keywords: geophytes, mammalian herbivory, pollination, reliable signals.

INTRODUCTION

The production of an inflorescence or floral display is not only beneficial as an advertisement for pollinators (Schaffer and Schaffer, 1979), it also bears the cost of being more evident to

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herbivores (Ehrlen, 1997). Hence, floral display may be selected for both pollinators and herbivores (Crawley, 1983; Marquis, 1992; Brody, 1997, Strauss, 1997). On the one hand, large floral displays enhance pollination (Schaffer and Schaffer, 1979; Cruzan *et al.*, 1988; Campbell, 1989; Klinkhamer *et al.*, 1994) because individuals that are more attractive will be visited by more pollinators, will have more pollen removed, and will therefore have greater mating success than individuals with fewer or less attractive flowers (Wyatt, 1982; Stephenson and Bertin, 1983; Stanton *et al.*, 1986; Zimmerman, 1988; Peakall and Handel, 1993; Snow, 1994; Murphy, 1998). Thus, sexual selection can occur if there are differences in pollen donor performance consistent across maternal plants (Snow and Spira, 1991; Marshall, 1998). On the other hand, attractiveness invites herbivores and thus increases risk of damage (Ehrlen, 1997), thereby reducing plant fitness (Harper, 1977; Crawley, 1983; Simms and Rausher, 1987; Allison, 1990; Mauricio *et al.*, 1993; Mutikainen and Delph, 1996; Delph *et al.*, 1997). Consequently, a conflict between maximizing the probability of pollination and minimizing the risk of being detected by herbivores may exist in plants (Englishloeb and Karban, 1992; Ehrlen, 1997).

According to the 'handicap theory' (Zahavi, 1975), a signal is an indicator of 'good genes' because it is an index of high general viability or condition, leading to survival advantages for the offspring (Krebs and Davies, 1993; Andersson, 1994). That is, albeit the cost of the trait, the 'good genes' are genes for the utilitarian aspects of survival and reproduction, rather than genes purely for attracting females, as assumed in the 'runaway' hypothesis (Fisher, 1930). If a floral display is a reliable signal (*sensu* Zahavi, 1975), a positive correlation should exist between the size of the inflorescence and the rewards for pollinators, because attractiveness to pollinators increases male fitness (Stanton *et al.*, 1986; Campbell, 1989; Fishbein and Venable, 1996). During autumn in the Mediterranean region, the number of flowering species and pollinators is low; the size of the inflorescence in this restricted 'market' (i.e. supply and demand) is an important 'discovery advertisement' (Herrera, 1982; Shmida and Dafni, 1989; Dafni and O'Toole, 1994). In this limited market, the foraging decisions of the pollinators are also conditioned on different factors: environmental variables, energy investment (handling costs, flight costs), and reward structure of the flower (Bosch *et al.*, 1997). Furthermore, selection for a larger floral display may result in more pollinator visits and diverse visitors, more rewards (pollen/nectar), more pollen donation/recipients, and more fruit/seed production (Dafni, 1992; Vaughton and Ramsey, 1995).

The desert lily *Pancratium sickenbergeri* (Amaryllidaceae) is a hysteranthous geophyte growing in the Negev Desert. It blooms in autumn, when the number of insects available to pollinate the flowers is low (Dafni and Werker, 1982). The inflorescence has 2–10 white flowers. The desert lily is exposed to different levels of herbivory by gazelles (*Gazelle dorcas*) during all its phenological stages (growth, dormancy, and flowering), The greatest impact the gazelles have on the lily populations in the Machmal sand dune is the consumption of flowers. A lily flower on this sand dune has less than a 0.0001 probability of surviving to the seed-producing stage (Saltz and Ward, 2000), and taller flowers have a higher probability of being selected by the gazelles (Saltz and Ward, 2000). Therefore, contrasting this extreme situation in the Machmal sand dune population with populations that experience less herbivory creates the possibility of testing the effects of herbivores and pollinators on the flowering strategy of the desert lily.

We sought to determine whether such advertisements constitute reliable signals. A signal must be costly otherwise all plants regardless of quality and benefit to potential pollinators would invest in such signals. If flower stalk height is a reliable signal for pollinators, does stalk height depend on the population-wide level of herbivory that the plant is subjected to?

We conducted several experiments to determine:

- the impact of herbivory level on flower stalk height;
- pollinator preference for flower stalk height;
- the effect of inflorescence size on rewards for pollinators; and
- the effect of flower stalk height on the production of fruits.

We predicted that there is stabilizing selection on the size of the inflorescence as a result of the pressure imposed by herbivores in one direction (for smaller size) in contrast to the pressure imposed by pollinators (for large size). Consequently, the optimum size of the inflorescence in each population will be different if there are differences in herbivory among populations. The cost of producing a taller stalk will be higher in populations with a high level of herbivory than in populations with a low level of herbivory (because of the greater probability of loss). In populations with a low level of herbivory, the benefit of attracting more pollinators will result in directional selection for taller flower stalks than in populations with a high level of herbivory. This is a unique study of a plant using the basic principles of behavioural ecology; essentially, it is the behavioural ecology of a plant.

METHODS

Study area

The study was conducted in different populations in two erosion cirques in the Negev Desert of Israel, Makhtesh Katan and Makhtesh Ramon. Makhtesh Katan is a small (30.6 km^2), oval-shaped cirque surrounded by steep walls. This area is characterized by an arid to extremely arid climate, with the scarce vegetation cover confined to the stream channels. Makhtesh Ramon is an anticlinal 200-km^2 erosion cirque on the southern boundary of the Negev highlands (see Saltz *et al.*, 1999). Makhtesh Ramon is typified by low rainfall (40–90 mm per year). The strong environmental changes (rainfall and temperature) are reflected in the vegetation (Ward *et al.*, 1993; Ward and Olsvig-Whittaker, 1993; Saltz *et al.*, 1999). In Makhtesh Ramon, we concentrated our study in two isolated, eastern lobes of the cirque, known as the Ardon and Machmal valleys. The predominantly western winds have created large sand deposits along the eastern walls of these valleys (Ward *et al.*, 1997). Loose sands can support dense populations of lilies, up to 2 per square metre, and they are attraction points for the dorcas gazelles (Ward and Saltz, 1994; Saltz and Ward, 2000). We can classify the different lily populations into those enduring high and low herbivory with a high degree of certainty based on 10 years of observations (see Ward and Saltz, 1994; Ward *et al.*, 1997; Saltz and Ward, 2000). Machmal dune lilies suffer the highest level of herbivory followed by Ardon dune. In Makhtesh Katan, the population of lilies grows in a small sandy valley and is exposed to a very low level of herbivory. Makhtesh Katan lilies do not suffer bulb or leaf herbivory, but they are exposed to flower herbivory sporadically (during drought years). In all these populations, we did not observe seed predation by insects during the study.

Study system

In the desert lily, leaves appear on the surface after the winter rains in late November and December (i.e. after the flowers have wilted) and may remain green until late spring, depending on rainfall and temperature. In spring, all the leaves dry up and fall off, leaving no above-ground material (Saltz and Ward, 2000). During winter, gazelles eat the leaf tip (± 1 cm) of the desert lily, and up to 100% of the plants may be affected. The tip is the only part of the leaf not defended by needle-like raphides of calcium oxalate (Ward *et al.*, 1997; Ruiz *et al.*, 2002a). Lily leaves have a basal meristem (Bold *et al.*, 1987) and, therefore, the growing point of the leaves is not affected by gazelle herbivory (Ward and Saltz, 1994). Summer foraging by gazelles has a negative impact on the desert lily (Ward and Saltz, 1994). Lilies in loose-sand dunes are subjected to a high level of herbivory. In the summer, gazelles dig for underground parts of lilies and may consume all or part of the bulb, which contains most of the plant's volume (Ward and Saltz, 1994). The greatest impact the gazelles have on the lily populations in sand dunes is the consumption of flowers. A lily flower on this sand dune has less than a 0.0001 probability of surviving to the seed-producing stage (Saltz and Ward, 2000). The inflorescence does not grow simultaneously with the leaves (hysteranthy). It blooms in the fall, producing one or two stalks (2–20 cm) with 2–10 flowers (6–12 cm) on each. Each fruit (2–7 cm^3) produces 50–200 relatively large seeds (6–10 mm, 0.5–4.0 g) that are dispersed by the wind.

No vegetative reproduction in the field has been recorded in 6 years of study of these lilies (Ward and Saltz, 1994; Saltz and Ward, 2000), although in greenhouse conditions, where plants were irrigated daily, we found vegetative reproduction. Preliminary studies indicated self-incompatibility in *P. sickenbergeri*. However, there could be differences between populations as in the case of *P. maritimun*, which is self-incompatible in Israel (Eisikowitch and Galil, 1971) but is self-compatible in Spain (Medrano *et al.*, 1999). In the desert lily, for normal seed set, insect pollination appears to be indispensable.

The dorcas gazelle, a small antelope, is a herbivore native to the deserts of the Middle East including southern Israel (Lawes and Nanni, 1993). Gazelles show a number of behavioural characteristics that are consistent with a long period of co-adaptation with the lily. They concentrate their activity in areas of high lily density, take the biggest plants with the most leaves in the winter, avoid those parts of the leaf defended by calcium oxalate, and in the summer dig for those plants that maximize the cost–benefit ratio of foraging (Ward and Saltz, 1994; Ward *et al.*, 2000). Gazelles prefer to feed on the lilies in loose sands. As sand compaction increases, the proportion of lilies that is dug up by gazelles decreases (Ward and Saltz, 1994). In addition, in the compacted-sand areas, the probability of a flowering lily reaching the seed-producing stage is 0.026, which is considerably higher than in the loose sands [1 : 30,000 (Saltz and Ward, 2000)]. Thus, although compact sands provide a poorer growing substrate, the level of herbivory is lower.

Experiments

To determine the effects of the herbivores and pollinators on reproductive success, we conducted different field experiments in three populations: Makhtesh Katan, Ardon valley and Machmal valley in Makhtesh Ramon. We conducted the experiments during the fall of 1998 and 1999. The desert lily blooms between the end of September and mid-November with a peak in mid-October. However, there is temporal variability among populations due to environmental factors that control flowering time, i.e. temperature and soil water (Boeken and Gutterman, 1986). The flowers in the inflorescences open sequentially and each flower is open for 2 days, during which there are no temporal differences in the functionality of the male and female components (anthers and stigma).

Survival and frequency distribution of floral stalk height

We tested for the effect of floral stalk height on inflorescence survival. In three populations with different levels of herbivory (Machmal dune, Machmal compact sand and loess), we counted the number of surviving inflorescences (with flowers in bud and/or anthesis) and measured flower stalk height. In addition, we estimated the frequency distribution of floral stalk heights using fenced plants in each population. We compared the frequency of flower stalk heights between populations (Makhtesh Katan and Machmal dune) with a Kolmogorov-Smirnov test.

Bulb energy

The energetic content of the bulb may determine the reproductive performance of the plant [i.e. inflorescence size (Theron and Jacobs, 1996)]. To test the effect of bulb herbivory on flower stalk height and plant fitness, we simulated herbivory of the bulb during the summer, with four treatment levels [cutting at the top (25% of the bulb biomass), in half (50%), at the bottom (80%) and a control (0%)], using 20 plants per treatment. Two years later, we measured the energetic content of the bulbs, the height and basal width of the flower stalk, and the production of fruits and seeds, as a measurement of current fitness. The energetic content of the bulb was measured using an oxygen bomb calorimeter (Parr). We used analysis of variance [ANOVA (Wilkinson, 1997)] to test for differences between treatments and a simple regression model to examine the effect of the energy content of the bulb on reproductive performance.

Pollinator preference

To determine whether pollinator preference depended on the height of the inflorescence, pollinator activity was observed as follows: In 1997, we watched visitors to lilies during 24 h in each population to determine which pollinators visited and the time of their visits. In 1998, over 3 days, we recorded the number of visits of pollinators between 05:30 to 08:30 h and 15:30 to 18:30 h. To determine whether the pollinator is attracted by a tall inflorescence or not, we marked the inflorescence that the pollinator visited and the inflorescence of the nearest neighbour that was not visited. Then we measured the height and basal width of the flower stalk and the total number of flowers of the visited and unvisited inflorescences. We counted the number of pairs in which the pollinator preferred the higher to the shorter flower stalk and vice versa; we compared the two populations of lilies using a χ^2 test. In 1999, for 5 days at the same times of day as in the previous year, we recorded the flower stalk height of the inflorescences visited and measured the size of the available inflorescences in an area measuring 15 × 15 m. Whether or not a plant was visited was treated as a binary variable, which we analysed using logistic regression with flower stalk height as an independent variable.

Floral traits and rewards

To determine the correlation between the height of the flower stalk and reproductive traits, we measured the number of ovules per flower and the number and size of flowers per flower stalk ($n = 60$ plants) in three populations (Makhtesh Katan, Ardon and Machmal valleys).

In addition, the rewards for the pollinators were measured as the number of pollen grains per plant and the energetic value of the nectar per flower (Dafni, 1992). To determine the number of pollen grains, we took the anthers from 20 new flowers, stored them in 70% ethanol, and stained them with methylene blue to count the pollen grains under light microscopy (Dafni, 1992). To estimate the energetic value of the nectar per flower, we measured the concentration of sugar and volume of nectar on 20 bagged new flowers every 3 h over 24 h ($n = 160$). We used bagged new flowers to avoid any effect of visitors or tissue damage. The concentration of sugar was measured with a hand refractometer (high-contrast type). Later, the energetic value was calculated according to Dafni (1992). We used a simple regression model to determine the correlation between flower stalk height and each of the floral traits. We performed an analysis of covariance (ANCOVA) to test the effect of populations and size of the flower stalk on the number of flowers per inflorescence.

Fruit and seed production

To determine the effect of the height of the flower stalk on the current fitness of the lilies, we measured the number and size of fruits and seeds relative to flower stalk height in each population. We performed an ANCOVA to test the effect of population and flower stalk height on the number of fruits and seeds.

RESULTS

Survival and frequency distribution of floral stalk height

There was a negative correlation between flower stalk height and inflorescence survival (with flowers in bud and/or anthesis) (Fig. 1). For populations growing on the soft sand (dune), survival was lower than for populations in compact sand. When we compared the size of inflorescences between populations, there was no significant difference in the frequency distribution of flower stalk height between populations (Kolmogorov-Smirnov, $D_{\mathrm{max}} = 0.88$, $P = 0.22$). However, there was a tendency in the distribution for a shorter flower stalk in populations with a high level of herbivory, as predicted under the stabilizing selection scenario (Fig. 2). In the high herbivory population, the size distribution was left skewed ($t_s = -0.018$, $P > 0.05$, d.f. = 17) and in the low herbivory population it was right skewed ($t_s = 0.458$, $P > 0.05$, d.f. = 17).

Bulb energy

There were significant differences between treatments in the energy content of the bulb ($F = 6.96$, $P < 0.001$, error d.f. = 75) and flower stalk height ($F = 5.79$, $P = 0.001$, error d.f. = 75; covariate = $\log_{10}$ initial bulb diameter). These differences were due to differences between the extreme herbivory treatment level (80%) and the other levels (Fig. 3). The total energy of the bulb showed a significant positive relationship with the number of fruits ($r = 0.26$, $F = 5.67$, $P = 0.01$, d.f. = 78) and the number of seeds per plant ($r = 0.24$, $F = 4.87$, $P = 0.03$, d.f. = 78). However, there were no significant relationships between flower stalk height and bulb energy ($F = 1.14$, $P = 0.29$, d.f. = 78), between the number of fruits and flower stalk height ($F = 2.25$, $P = 0.36$, d.f. = 78), or between the number of seeds and flower stalk height ($F = 2.02$, $P = 0.16$, d.f. = 78) in this cutting experiment. That is, the energy

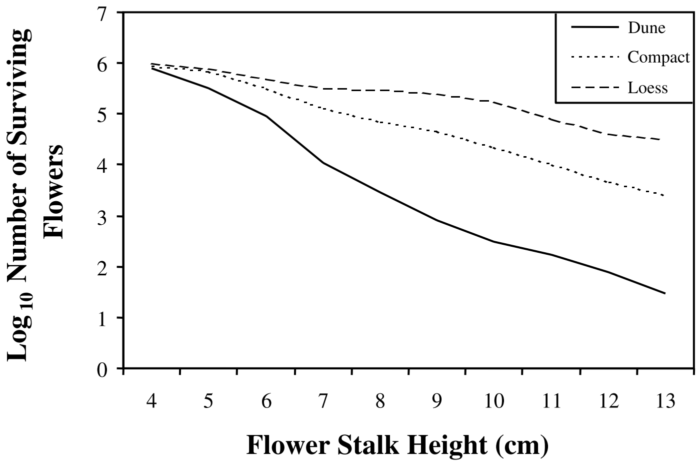

Fig. 1. Log_{10} number of surviving flowers against flower stalk height for three populations in Machmal with different types of sand and levels of herbivory. Dune = high herbivory; compact = low herbivory; loess = very low herbivory.

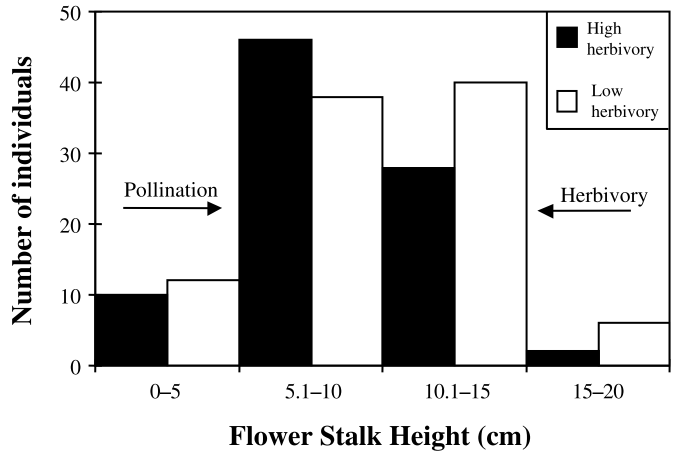

Fig. 2. Frequency distribution of flower stalk height in relation to the level of herbivory (high, low). In populations with a high level of herbivory, selection for herbivory will produce a shorter inflorescence. In populations with a low level of herbivory, selection for pollination will produce a taller inflorescence.

stored in the bulb affects the production of the inflorescence, fruits and seeds, but among those plants that can reproduce there is no clear relationship between bulb energy and investment in flower stalk size.

Pollinator preference

The flowers open during sunset over 2 days and are visited by moths (Sphingidae), butterflies (Pieridae), bees (*Eucera* sp.), and syrphid flies (Syrphidae) at different times of the day. The hawk moth, *Macroglossum stellatarum* (Sphingidae), appears to play the main role in

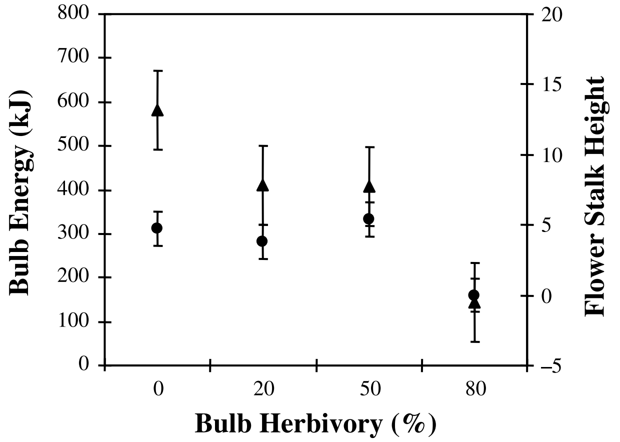

Fig. 3. Means and standard errors for the energy content of the bulb and flower stalk height for different amounts of bulb removed, simulating herbivory by gazelles. ● = bulb energy; ▲ = flower stalk height.

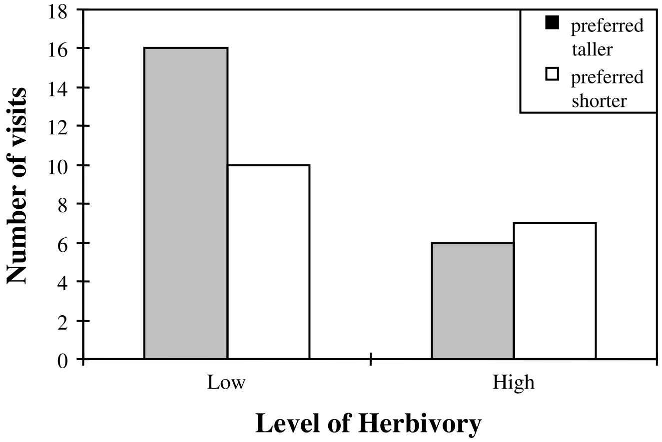

Fig. 4. Pollinator preference of flower stalk height in two populations with different levels of herbivory: Low = Katan; high = Machmal. Number of visits (preferred taller inflorescence vs. preferred shorter inflorescence).

the pollination of the desert lily. There were no significant differences in the pollinators' preferences for the size of flower stalk between populations in 1998 ($\chi^2 = 2.00$, $P = 0.15$, d.f. = 1, sample size = 39) (Fig. 4) and 1999 (logistic regression, $P > 0.05$, d.f. = 47). Further observations are necessary to differentiate between the preferences of each species of pollinator.

Floral traits and rewards

There was a significant positive relationship between flower length (an index of floral display size) and flower stalk height ($r = 0.47$, $F = 49.7$, $P < 0.001$, d.f. = 59) (Fig. 5). Similarly, we found a significant positive relationship between the number of pollen grains and the total

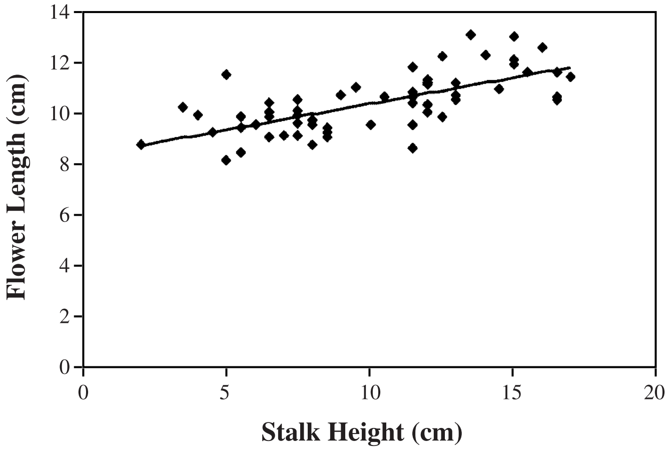

Fig. 5. Relationship between flower length (cm) and flower stalk height (cm) ($r = 0.47$, $F = 49.7$, $P < 0.001$, d.f. = 59).

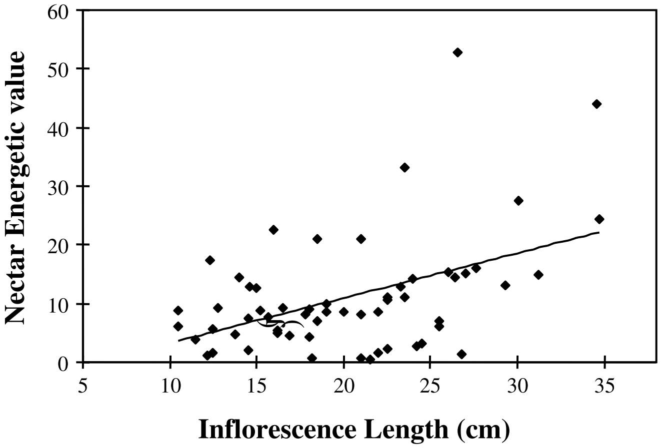

Fig. 6. Relationship between nectar energetic value (J) and inflorescence length (cm) ($r = 0.46$, $F = 14.97$, $P < 0.001$, d.f. = 57).

length of the inflorescence ($r = 0.50$, $F = 6.11$, $P = 0.02$, d.f. = 18) and between the energetic content of the nectar and the total length of the inflorescence ($r = 0.46$, $F = 14.97$, $P < 0.001$, d.f. = 57) (Fig. 6). That is, taller inflorescences produced more rewards for pollinators than smaller inflorescences. In addition, the analysis of covariance showed a significant effect of flower stalk height (covariate) on the number of flowers ($F = 17.84$, $P < 0.001$, d.f. = 1), but no significant difference in the number of flowers per flower stalk among populations ($F = 0.16$, $P = 0.85$, d.f. = 2).

Fruit and seed production

The analysis of covariance showed a significant effect of population and flower stalk height on the number of fruits and number of seeds per plant (Tables 1 and 2). There was a

Table 1. Results of ANCOVA for the $\log_{10}$ number of fruits against population and $\log_{10}$ flower stalk height (population: Katan, Ardon, Machmal)

Source	d.f.	MS	*F*	*P*
Population	2	0.79	4.04	0.019
Log_{10} flower stalk height	1	8.79	44.95	<0.001
Population × $\log_{10}$ flower stalk height	2	0.99	5.09	0.007
Error	150	0.19		

Table 2. Results of ANCOVA for the $\log_{10}$ number of seeds against population and $\log_{10}$ flower stalk height (population: Katan, Machmal)

Source	d.f.	MS	*F*	*P*
Population	1	2.05	8.54	0.005
Log_{10} flower stalk height	1	18.91	78.83	<0.001
Population × $\log_{10}$ flower stalk height	1	2.11	8.81	0.004
Error	78	0.24		

significant interaction between population and flower stalk height on the number of fruits and seeds. This result shows that there is variability in fruit and seed production due to the size of the flower stalk and that this variability differs among the populations (with different herbivory levels). Similarly, there was a significant positive correlation between fruit volume and flower stalk height ($r = 0.40$, $F = 10.61$, $P = 0.002$, d.f. = 59).

DISCUSSION

In the desert lily, the size of the inflorescence is a highly variable character. This variability could be a phenotypic result of differences in resource availability to the plant (Fishbein and Venable, 1996; Saltz and Ward, 2000). In many hysteranthous geophytes an accumulation of storage material during the previous winter season is a prerequisite for reaching the 'critical mass' (energy/nutrient reserves) necessary to invest in subsequent reproduction (Dafni *et al.*, 1981). This is the case in *Pancratium sickenbergeri*, in which we found that a threshold energy content of the bulb must be exceeded to produce an inflorescence (Fig. 3). Above the critical bulb mass, we did not find that size of the flower stalk depends on the energy content of the bulb. This suggests that the size of the flower stalk is independent of environmental factors, such as rain during the previous winter when storage of resources occurs for the subsequent flowering season. In addition, the reserves accumulated in one year must provide for flowering and leaf production in the following year (Dafni *et al.*, 1981). Nevertheless, we did not find a significant relationship between the number of fruits and bulb energy or between number of seeds and bulb energy.

In general, the attractiveness of the inflorescence to gazelles can be considered as a density-dependent factor. That is, a large number of individuals is more attractive to herbivores than few individuals regardless of the size of the inflorescence. For example, sand dune populations (high density) are more attractive to gazelles than compact sand populations (low density) (Ward and Saltz, 1994; Saltz and Ward, 2000). However, the number of surviving flowers decreased when the length of the flower stalk increased in both low and high herbivory populations (Fig. 1). In other words, there was an effect of inflorescence size over and above that of plant density.

Pancratium sickenbergeri possesses vegetative and chemical defence strategies in bulbs and leaves to maintain the fitness of the plant in the face of gazelle herbivory (Ward *et al.*, 1997; Ruiz *et al.*, 2002b). However, no such adaptation has evolved for the inflorescence [the consumption of the inflorescence has the greatest negative impact on the plant (Saltz and Ward, 2000)]. In general, the production of attraction features (nectar, corollas, etc.) may be costly, and these costs may impinge on the resources available for other plant functions, including plant defence (Strauss, 1997). That is, investment in a large floral display in the desert lily may have the cost of reduced or no investment in defence. Therefore, the high investment in the production of a large inflorescence to attract pollinators can be considered as a strategy that maintains fitness [plants with tall stalks may be more apparent to pollinators and thus more likely to be pollinated than plants with short stalks (Cruzan *et al.*, 1988; Mitchell, 1994)].

Although sexual selection ideas are widespread in botany (Andersson and Iwasa, 1996) and signal selection examples have been reported for many species of birds (see Zahavi and Zahavi, 1997), our results provide unique examples of a reliable signal in plants. Even though a big floral display has a survival cost (because it is more evident to gazelles), we found that the size of the flower stalk appears to be a reliable signal (*sensu* Zahavi, 1975) for pollinators because rewards such as nectar and pollen increase when the total size of the inflorescence increases (Fig. 6). Insects respond more to floral reward than floral morphology and floral rewards affect pollinator visitation patterns (Delph and Lively, 1992; Bosch *et al.*, 1997). Pollinators are able to categorize flower stalks in terms of size (Schaffer and Schaffer, 1979). However, we did not find a strong pollinator preference for taller stalks. The pollinator preference for taller stalks is a complex foraging decision (Dafni, 1992) that includes the availability of inflorescences in the population as a result of the level of herbivory. For instance, in the population with a high level of herbivory where the availability of flowers is low due to gazelle predation (Machmal dune), there were no clear preferences (i.e. the pollinator does not have as much to choose from). In contrast, in a population with a low level of herbivory, where the density of flowers is high (Katan), there was a preference for taller stalks.

It is clear that different species of pollinators, such as moths, butterflies, and bees, may have different preferences for inflorescence size. For example, Cruzan *et al.* (1988) found that insect visitors to *Phyla incisa* inflorescences differed in their foraging behaviours. Honeybees, native bees, and beeflies were more selective than butterflies and honeybees, whereas native bees and butterflies selected larger inflorescences than expected from the size distribution of inflorescences available. Furthermore, Schaffer and Schaffer (1979) showed in a co-evolutionary model applied to the evolution of plant reproductive expenditure and pollinator foraging strategies in yuccas and agaves that large bees identified resources as a function of the size of the flower stalk to maximize their rate of caloric intake. Therefore, the pollinator's foraging behaviour alters the shape of the trade-off function, and thus the optimal reproductive expenditure for the plants. In particular, increasing pollinator preference for large flower stalks selects for increased reproductive investment. This result also suggests that increased availability of resources will lead to further increases in selectivity by the pollinators.

The differences in inflorescence size and number of seeds between populations of lilies indicate an effect of herbivores and pollinators on the reproductive strategies of the desert lily, thereby creating sufficient variability to produce a genotype × environment interaction, and hence local adaptation (Ward and Saltz, 1994). Consequently, a long-term study is required to determine the additive genetic variance of the size of the flower stalk in the desert lily. A common-garden experiment with seeds from different populations will be necessary to ascertain whether genotype × environment interactions have evolved.

ACKNOWLEDGEMENTS

We thank Iris Musli, Esther Guggenheim, Dror Zchori, Iris Schmidt, and Michal Laniado for assistance in the field. Yael Lubin provided fruitful discussion about sexual selection. Avi Golan loaned a microscope. This research was supported by the Israel Science Foundation. This is publication #438 of the Mitrani Department of Desert Ecology.

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