

# Variability in nectar production and standing crop, and their relation to pollinator visits in a Mediterranean shrub

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**Abstract** Nectar standing crops in flowers within an individual plant are often highly variable. This variability may be a by-product of the foraging activity of insect pollinators. Alternatively, plants may be selected to produce highly variable rewards to reduce consecutive visitation by risk-averse pollinators, thus diminishing within-plant pollen transfer. This study evaluated the roles of pollinator control vs. plant control over nectar variability in the bee-pollinated shrub *Rosmarinus officinalis* L. (Lamiaceae). We sampled nectar production, standing crop and pollinator visits in three shrubs of one population over 17 days during one blooming season. Nectar production rates were highly variable ( $CV = 1.48$ ), and increased after rainy days. Nectar standing crops were even

more variable ( $CV = 2.16$ ), decreased with increasing temperatures, and increased with time since the last rain. Pollinator visit rates decreased with variability in nectar standing crops, increased with flower number per shrub, and were unaffected by variability in nectar production rates. Repeated sampling of marked flowers revealed no correlation between their nectar standing crops and production rates. These findings support the role of reward variance in reducing pollinator visits, but suggest that plants are not in complete control of this variability. Rather, plant-generated variability can be modified by intensive foraging activity of pollinators. Such pollinator control over nectar variability is likely to reduce the selective advantage of plant-generated reward variation.

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## Introduction

Insect-pollinated plants that are visited by a large number of pollinator individuals gain reproductive benefits, due to increased import and export of pollen. Repeated visits of the same pollinator to a plant, on the other hand, increase within-plant pollen transfer (geitonogamy), which is genetically equivalent to self-pollination. Self-incompatibility mechanisms prevent geitonogamous fertilization in some plants. In other species, geitonogamous fertilization does occur, but leads to lower-quality offspring. Both effects may reduce female fitness. Geitonogamy can also decrease male fitness because of reduced export of pollen to other plants. It has been therefore suggested that plant traits that reduce geitonogamous pollination would be selectively advantageous (de Jong et al. 1993; Reusch

2001; Barrett 2003). When pollinators are abundant, the optimal situation for plants would be to receive visits from a large number of pollinator individuals, but have each of them visit only a small number of flowers in succession (Klinkhamer et al. 1994).

Pollinators often visit only a small fraction of the flowers available to them, before shifting to a different individual (Klinkhamer and de Jong 1990; Ohashi and Yahara 2001). Encounters with low or zero rewards have been shown to promote patch shifts by bees in laboratory situations, and in natural settings (Kadmon and Shmida 1992; Keasar et al. 2002). Furthermore, bees often forage in a risk averse-manner, i.e. prefer food sources with low variance over high-variance sources with equal mean rewards (Kacelnik and Bateson 1996; Shafir 2000). These observations underlie the hypothesis that within-plant variation in nectar production rates may reduce geitonogamy levels, so that such variation is favored by selection (Rathcke 1992; Pappers et al. 1999; Biernaskie et al. 2002). This hypothesis predicts that variable within-plant nectar production rates would generate variability in nectar standing crops. This variability, in turn, would reduce visitation by insect pollinators.

Considerable within-plant variability in nectar production rates was measured in a number of species (Feinsinger 1983; Zimmerman and Pyke 1986; Herrera and Soriguer 1983; Marden 1984; Boose 1997). Nectar standing crops within plants are variable as well, and show a patchy spatial distribution (Shmida and Kadmon 1991). Nectar standing crops are affected both by the plant's rate of nectar production, and by nectar consumption by pollinators. Bees forage for nectar in an area-restricted manner, i.e. fly shorter distances after visiting nectar-rich flowers, and longer distances after visiting flowers with low rewards (Keasar et al. 1996; Burns and Thomson 2006). This movement pattern leads to patchy exploitation of the nectar, and generates patchiness in nectar standing crops even in the absence of variability in nectar production (Motro and Shmida 1995). It is not straightforward, therefore, to deduce variability in nectar production from measuring variability in nectar standing crops. The existence of such variability may be due to nectar production by the plant, to pollinator activity, or to a combination of both factors. Combined measurements of nectar production, nectar standing crops, and pollinator activity are needed to understand whether variability in nectar secretion by plants can play a role in restricting pollinator visitation and geitonogamy.

In the present study we assessed nectar production, standing crop and insect visits in *Rosmarinus officinalis* L. (Lamiaceae). This Mediterranean bee-pollinated shrub simultaneously produces several hundred protandrous, self-compatible flowers, and suffers inbreeding depression due

to geitonogamous pollination (Hidalgo and Uberta 2001). We recorded the number of open flowers per shrub on each observation day, because plant size may affect nectar production (Pleasants and Chaplin 1983) and pollinator visit rates (Brody and Mitchell 1997; Goulson et al. 1998). In addition, we recorded rainfall prior to sampling sessions, and temperature during sampling, since these variables may affect nectar production (Wyatt et al. 1992; Carroll et al. 2001; Leiss and Klinkhamer 2005).

We asked the following questions regarding this model plant:

1. What is the extent of within-shrub variability in nectar production and standing crops?
2. Does within-plant variability in nectar production and standing crops affect pollinator visitation?

## Material and methods

We repeatedly measured nectar production and pollinator visits in three plants of *Rosmarinus officinalis* in Kibbutz Hatzor, Central Israel. *R. officinalis* was the dominant flowering plant in the study area during the whole study period. Plants in our study populations were in bloom from October to March. Corolla length and width were  $1.37 \pm 0.18$  (SD) and  $0.50 \pm 0.07$  cm, respectively, and floral tube length was  $1.04 \pm 0.25$  cm ( $n = 50$ ). Nectar and insect visit data were collected between 8 am and 2 pm on 17 days during October–December 2002. On the start of each observation session (8 am), we recorded nectar standing crop in 10 flowers per plant using 1- $\mu$ l micropipettes. This 10-flower sample constituted five pairs of nearest-neighboring flowers from haphazardly determined locations on the plant. We calculated the correlation in nectar standing crops within and between flower pairs as a measure of within-plant patchiness in nectar distribution. We bagged the sampled, depleted flowers with bridal-veil netting (Wyatt et al. 1992), and harvested them again after 3 h (11 am), 6 h (2 pm) or 24 h (8 am on the following morning). We sampled 10 flowers (3–4 per shrub) at each time point. The nectar that accumulated in the sampled flowers represents the plant's 3 h, 6 h or 24 h nectar production. We divided the produced nectar volume by the covering time to obtain nectar production rates. We determined sugar concentration in nectar samples that exceeded 1/3  $\mu$ l with a Bellingham–Stanley hand-held refractometer. This was done for samples taken for nectar standing crops, as well as for samples taken for 3-, 6- and 24 h nectar production. We noted the time of concentration measurements, since nectar concentrations may change during the day. We were not able to determine sugar concentrations in nectar volumes of less than 1/3  $\mu$ l.

We counted the number of insect visits to a sample of 100 flowers in each plant during a 10-min observation period. Counts were performed during peak pollinator activity hours, between 10 am and 12 pm, on the same plants that were used for nectar measurements. We performed one count per plant on each observation day, totaling 51 counts. We classified the pollinators into the following functional groups: honeybees, large bees (larger than honeybees), small bees (smaller than honeybees), flies, butterflies and beetles.

### Data analysis

We used ANOVA to test for the effect of bagging duration on hourly nectar production rates. We treated the variable “plant” as a random factor in the ANOVA, because repeated nectar production samples from the same plants are not independent measurements. We then tested for the effects of sampling date, plant, and pair within plant on nectar production rates using a general linear model. Sampling date (17 possible values) was treated as a fixed factor, and plant (three possible values) was treated as a random factor. Flower pair (five possible values) was considered as a nested factor within a given plant and sampling date. Bagging duration was treated as a covariate, and the variance between flowers within a pair was treated as the residual error term. We tested for correlations in nectar production between pair members using Pearson’s correlations.

Since nectar standing crop data were obtained in unbagged flowers, we only considered the effects of sampling date, plant and flower pair on nectar standing crops. As with the nectar production analysis, we used a general linear model with date (17 possible values) defined as a fixed factor, plant (three possible values) defined as a random factor, and flower pair (five possible values) defined as a nested factor within date and plant.

We used regression models to evaluate the contributions of the following environmental variables on nectar standing crop and production: recent rainfall (mm rain on the last rain event before observation), the number of days elapsed since this rain event, minimal and maximal temperatures during observation. We calculated the mean nectar standing crop and production rate, and their standard deviations, corresponding to each of the 51 observations (17 days  $\times$  3 plants) of insect visits. We then regressed the number of visits per observation against (1) the mean nectar standing crop (2) the standard deviation of the standing crop, and (3) the number of flowers per plant. The data points for these regressions are not independent, because they were collected repeatedly from the same three plants. We therefore tested the effects of plant (treated as a random variable) on the number of insect visits per

observation. We used partial regression plots to show the effects of flower number and nectar standing crop variability on insect visit rates, after taking into account the effect of the plant variable (Figs. 2, 3).

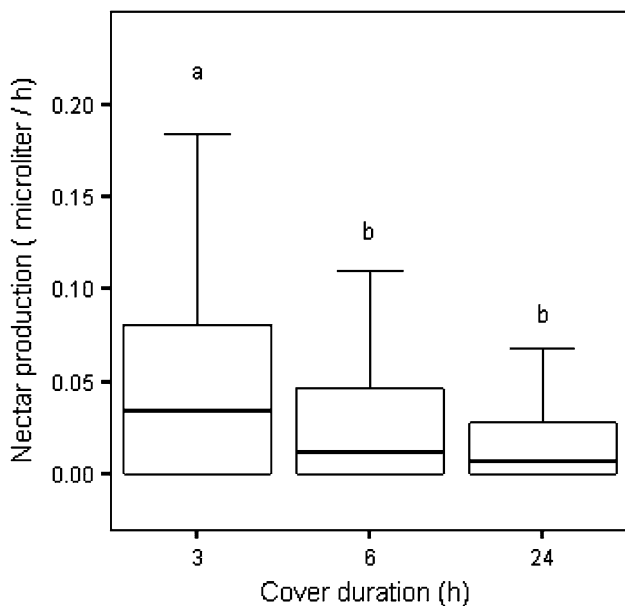
Nectar production and standing crop data were normalized through logarithmic transformation prior to analysis. Visitor count data were square-root transformed. We used SPSS version 15.0 for statistical analyses.

## Results

### Nectar production

Mean ( $\pm$ SD) total nectar volumes produced during 3, 6 and 24 h of covering were  $0.17 \pm 0.24 \mu\text{l}$ ,  $0.18 \pm 0.26 \mu\text{l}$  and  $0.43 \pm 0.60 \mu\text{l}$ , respectively. Accordingly, the volume produced per hour was highest for flowers covered for 3 h (8 am–11 am), and lowest for the 24-h covering period (8 am–8 am) (Fig. 1). The effect of covering period on nectar production was highly significant ( $F_{2,335} = 45.90$ ,  $P < 0.001$ ). Hourly nectar production rates varied significantly among flower pairs, but not among sampling dates and plants. The interaction between sampling date and plant was significant, however. (GLM:  $F_{15,366} = 1.38$ ,  $P = 0.16$  for date;  $F_{2,366} = 1.37$ ,  $P = 0.26$  for plant;  $F_{30,366} = 3.20$ ,  $P < 0.0001$  for date  $\times$  plant interaction;  $F_{4,366} = 3.18$ ,  $P = 0.01$  for flower pair; covering duration treated as a covariate). Covering time did not interact significantly with plant ( $F_{2,366} = 0.53$ ,  $P = 0.59$ ) and with sampling date ( $F_{15,366} = 1.01$ ,  $P = 0.44$ ). 30.6% of the flowers covered for 3 h, 39.4% of flowers covered for 6 h, and 31.2% of the flowers covered for 24 h did not produce any nectar during the covering period.

For the remaining analyses we used only the nectar production data that were obtained from flowers covered for 3 h. We report mainly on the 3-h covering period for two reasons: First, nectar production pattern observed in Fig. 1 may be due to higher production rates between 8 and 11 am than later in the day. Since peak pollinator activity occurred during these hours as well, these rates seem relevant for explaining the majority of pollinator visits, and for exploring plant-produced versus visitor-generated variability. Second, the effect of covering time on hourly nectar production rates may reflect inhibitory effects of nectar accumulation within the nectaries on further production (Castellanos et al. 2002). The high rate of pollinator visits to *R. officinalis* (see below) probably prevented nectar accumulation in flowers of our study population. Hourly nectar production rates based on 6-h or 24-h netting may therefore underestimate production rates in flowers exposed to pollinators.



**Fig. 1** Box-plot of mean hourly nectar production in flowers that were covered to exclude insect visits for 3, 6 or 24 h. The height of the boxes denotes the interquartile range. Medians are marked by thick lines within the boxes. Error bars are 1 SD. Data were collected from 170 flowers for each covering period. Production rates that significantly differ from each other in Tukey Post-Hoc tests are denoted by different letters

The hourly nectar production rate (based on 3-h measurements) was highly variable ( $CV = 1.48$ ,  $n = 170$  flowers). Mean w/w sugar concentration in the nectar was  $70.6 \pm 8.5\%$  ( $CV = 0.12$ ,  $n = 65$  flowers). Thus, the variability in nectar concentration was significantly lower than the variability in volumes ( $F_{117,64} = 10.04$ ,  $P < 0.001$ , Lewontin's (1966) test for equality of CVs). Nectar production rates were significantly correlated between flower-pair members within a plant ( $n = 85$  flower pairs, Pearson's correlation = 0.39,  $P < 0.001$ ). They were significantly affected by the amount of the last rain before sampling. The number of days elapsed since the rain, the minimum and the maximum temperatures on the day of sampling, did not significantly affect nectar production rates (Table 1).

#### Nectar standing crops

Mean nectar standing crop was  $0.32 \pm 0.69 \mu\text{l}$  (SD,  $n = 510$  flowers,  $CV = 2.16$ ), thus nectar standing crops were highly variable. 56% of the sampled flowers contained no measurable nectar, while 1.4% of the samples contained more than  $3 \mu\text{l}$  nectar, reflecting an extremely skewed distribution of standing crops. The CV in nectar standing crops was significantly higher than the CV in hourly nectar production rates ( $F_{75,117} = 2.14$ ,  $P < 0.001$ , Lewontin's (1966) test for equality of coefficients of

**Table 1** Regression results for nectar production rates

Model	Sum of squares	df	Mean square	F	P-value
Regression	0.078	4	0.020	2.692	0.034
Residual	0.910	125	0.007		
Total	0.989	129			
Model variable	Coefficient	t	P-value		
Regression model coefficients					
Amount of last rain	0.327	3.070	0.003		
Days after rain	0.082	0.643	0.521		
Minimum temperature	0.014	0.100	0.921		
Maximum temperature	0.045	0.272	0.786		

variation). Nectar standing crops were positively correlated between flower-pair members, similarly to nectar production rates ( $n = 255$  flower pairs, Pearson's correlation coefficient = 0.42,  $P < 0.001$ ). Nectar standing crops varied significantly among sampling dates, but not among plants or flower pairs (GLM:  $F_{16,267} = 22.68$ ,  $P < 0.001$  for date;  $F_{2,407} = 1.24$ ,  $P = 0.29$  for plant;  $F_{12,267} = 0.69$ ,  $P = 0.76$  for date  $\times$  plant interaction;  $F_{222,267} = 1.05$ ,  $P = 0.35$  for flower pair). Nectar standing crops and hourly nectar production rates, measured in the same flowers, were not correlated (Pearson correlations coefficients:  $-0.05$ ,  $P = 0.49$ ;  $-0.06$ ,  $P = 0.45$ ;  $0.07$ ,  $P = 0.34$  for flowers covered for 3, 6 and 24 h respectively,  $n = 170$  flowers for each covering period). Nectar standing crops decreased as maximal air temperatures increased, and increased with time since the last rain, but were not affected by the amount of rain or minimal air temperatures (Table 2).

#### Pollinator visits

We observed  $63.4 \pm 8.1$  (mean  $\pm$  SE) flower visits by insects on 100 flowers during the 10-min observation

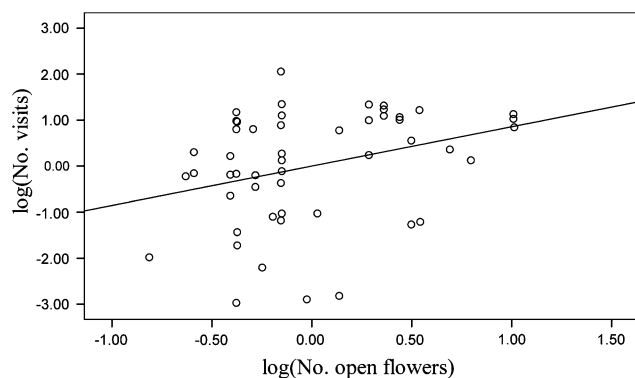
**Table 2** Regression results for nectar standing crops

Model	Sum of squares	df	Mean square	F	P-value
Regression	16.951	4	4.238	2.452	0.049
Residual	254.103	147	1.729		
Total	271.054	151			
Model variable	Coefficient	t	P-value		
Regression model coefficients					
Amount of last rain	-0.105	-1.166	0.246		
Days after rain	0.264	2.230	0.027		
Minimum temperature	0.237	1.898	0.060		
Maximum temperature	-0.429	-2.719	0.008		

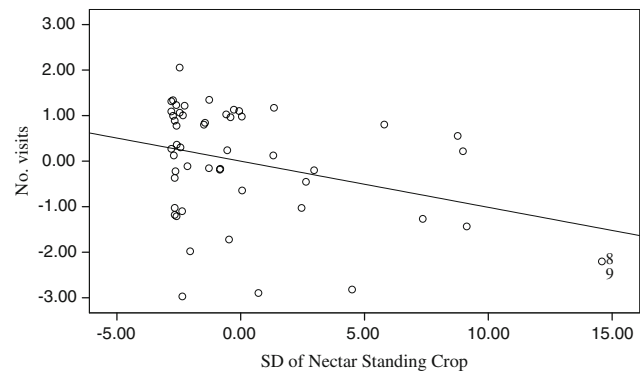
periods ( $n = 51$  observations). This is equivalent to an average of 3.8 visits per flower per hour. We did not record the number of pollinator approaches to the shrubs, and lengths of visit bouts within them. Honeybees were the most abundant visitors (57.1% of all visits). Small bees accounted for 36.3% of the visits, and the remaining groups of pollinators visited the flowers at low frequencies. The number of insect visits significantly increased with increasing number of flowers per plant (Fig. 2,  $t_{50} = 2.30$ ,  $P = 0.03$ ), but were not affected by plant identity ( $t_{50} = -0.64$ ,  $P = 0.53$ ). Insect visit rates decreased with the SD of nectar standing crops (Fig. 3,  $t_{50} = -2.34$ ,  $P = 0.03$ ), and were not affected by plant identity ( $t_{50} = 0.34$ ,  $P = 0.73$ ). Mean nectar standing crops did not significantly affect the number of insect visits ( $t_{50} = -1.75$ ,  $P = 0.09$ ). As in previous analyses, the plant variable did not significantly affect insect visit rates ( $t_{50} = 0.47$ ,  $P = 0.64$ ).

## Discussion

Our study combines data on variability in nectar production and standing crops, and their relations with pollinator visits, in a single set of field observations. Our observations of *R. officinalis* demonstrate high within-plant variation in nectar production rates. Within-plant variability in nectar standing crops was even higher, as indicated by a larger coefficient of variation. Pollinator visitation was negatively correlated with the variation in nectar standing crop, but was not related to the variability in nectar production. These findings suggest that the plants' nectar production patterns were not the only source for variability in our



**Fig. 2** Partial regression plot for the effect of the number of open flowers per shrub on the number of pollinator visits in a 100-flower sample during a 10-min observation period. The full regression model also included plant, the mean and the standard deviation of nectar standing crops as independent variables. Data were log-transformed to linearize the exponential function between flower number and visit number. The slope of the linear regression line corresponds to the exponent (de Jong and Klinkhamer 2005).  $n = 51$  observations,  $Y = 0.663x + 36.17$ ,  $r^2 = 0.09$ ,  $P < 0.001$



**Fig. 3** Partial regression plot for the effect of the within-shrub nectar standing crop variability, expressed as the standard deviation of the mean reward volume, on the number of pollinator visits. The full regression model also included plant, mean nectar standing crop and number of open flowers as independent variables. Visits were recorded in a 100-flower sample during 10-min observation periods.  $n = 51$  observations,  $Y = -3.98x + 72.48$ ,  $r^2 = 0.08$ ,  $P = 0.047$

study. Rather, the foraging activity of pollinators increased the plant-generated variability in nectar standing crops. Such increased variability, in turn, may have reduced further pollinator visits. Thus, variability in nectar standing crops could be both cause and effect of insect visitation patterns. Nevertheless, about 1/3 of the flowers did not produce any nectar while they were covered. These empty flowers are clearly part of the plants' contribution to the variability in nectar standing crops, since zero nectar cannot be altered by pollinators. A possible interpretation of these observations is that variation in nectar production rate creates some initial variance in nectar standing crop, which reduces insect visitation adaptively (by reducing geitonogamy). Next, pollinator visitation may further increase standing crop variance, and further limit geitonogamy, by creating localized pools of depleted flowers.

Alternatively, if pollinators mainly react to nectar variability created by their own foraging activity, then plant-generated variability in nectar production should not be favored by selection. Such variability would then merely reflect between-flower differences in sexual phase (Carlson and Harms 2006), flower age (Pleasants 1983; Zimmerman and Pyke 1986) or microhabitat conditions. For example, since blooming in *R. officinalis* advances along the inflorescence from bottom to top, neighboring flowers that were sampled at different heights along the inflorescence may differ in age and sexual phase, and thus also in nectar production rates.

Neighboring flowers within a plant were positively correlated in nectar production rates as well as in nectar standing crops, but we found no correlation between production rate and standing crop within a single flower. In other words, the flowers that had the highest production rates when bagged did not necessarily contain the highest

standing crops when exposed to pollinators. A possible interpretation of this finding is that nectar production rate in each flower is variable over its lifetime, and that measurement of production and standing crop at different points in time reflects this variability. Flower age was shown to affect nectar production rates in some plants, supporting this possibility (Southwick and Southwick 1983; Galetto et al. 1994). An alternative interpretation is that the variability in standing crop is partly generated by pollinator activity, while the variability in production is only due to the plant. Repeated measurements of nectar production along the blooming duration of individual flowers are needed to distinguish between these interpretations.

Our study corroborates previous findings of environmental effects on floral nectar traits (Wyatt et al. 1992; Carroll et al. 2001; Leiss and Klinkhamer 2005). Interestingly, nectar production rates and standing crops were affected by different environmental parameters: rainfall was the most important predictor of nectar production rates, while temperature best predicted nectar standing crops. Increased temperatures may have allowed higher pollinator activity, leading to increased nectar consumption and reduced standing crops. A second possible effect of elevated temperature is increased nectar evaporation from flowers, leading to reduced standing crops. However, increased evaporation should be associated with elevated nectar concentrations. The low variability in nectar concentrations recorded in our study makes this interpretation less likely. Contrary to some previous work (Pleasants and Chaplin 1983), nectar parameters were not affected by the number of blooming flowers in our study system. Flower number significantly influenced pollinator attraction, on the other hand, as previously observed for other plant species (Robertson and McNair 1995; Goulson et al. 1998).

Insect visitation in our study was negatively related to variability in nectar standing crops, but was not related to nectar production. These observations suggest that the variability in nectar production may not suffice to affect insect visitation, and may be masked by the higher variability in standing crops. The variability in production rates is plant-generated, while the variability in standing crops is generated both by plants and by pollinator activity. This implies that pollinator-generated variation has important effects on pollinator foraging, possibly overriding the effects of plant-generated variation. Pollinator-generated variability in nectar rewards may thus reduce the selective benefit of plant-generated variability as a strategy to decrease geitonogamy.

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