Floral Heat Rewards and Direct Benefits to Insect Pollinators

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ABSTRACT Some Arctic and alpine flowers are bowl-shaped solar collectors whose temperatures are significantly warmer than ambient air temperatures. One explanation for this trait is that it represents plant–pollinator coadaptation. Just as flowers providing nectar and pollen may be attractive to insects, warm flowers providing thermal refuges in a cold environment may also serve to attract insects. In this article I present data on the actual benefits obtainable to insects basking in flowers or on the ground, and I demonstrate that if insects seek heat alone, then warm flowers cannot be explained by plant–pollinator coevolution. Instead, exclusively botanical explanations for the origins of this trait seem more reasonable.

KEY WORDS *Ranunculus adoneus*, alpine insects, heliotropism, insect thermoregulation, insect basking, pollinator rewards

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FOR FLYING INSECTS in tundra environments, low temperatures may be as important a constraint as low food availability. For many insects, power output from wing muscles is insufficient to permit flight unless the muscles are operating at temperatures of 35–40°C (Heinrich 1993). Flying insects living in low-temperature environments can remain active either by producing endothermic heat or by restricting their activities to times or locations when and where ambient temperatures permit flight (Kevan and Shorthouse 1970; Morgan and Heinrich 1987; Heinrich 1979, 1993). Providing a visiting insect with warmth in a cold environment might, for entomophilous plants, promote pollination as effectively as providing food rewards.

The flowers of some tundra angiosperms are known to function as small *solar furnaces* or heat collectors, with temperatures up to 10°C warmer than ambient air temperature (Kevan 1972, 1975; Stanton and Galen 1989). Often, insects visit such flowers and appear to bask; basking insects may be passively thermoregulating (Hocking and Sharplin 1965, Hocking 1968, Heinrich and Raven 1972, Heinrich 1975, Kevan 1975, Ring and Tesar 1981). Several authors have commented on the existence of solar-furnace flowers in tundra communities, suggesting that in addition to direct benefits to plants, flowers with an architecture enabling them to capture solar radiation (hereafter referred to as warm flowers) are able to modify pollinator behavior, thereby enhancing plant reproductive success (Hocking and Sharplin 1965; Kevan 1972, 1975; Smith 1975). Selection for enhanced pollination success could have favored the evolution of flowers that collect solar radiation and provide heat rewards for visiting insects.

Materials and Methods

One test of the hypothesis that insect visitation could exert strong selective pressure favoring warm, bowl-shaped flowers is to determine whether or not the net thermal gain realized by insects visiting such flowers is as good as or better than thermal benefits obtainable elsewhere. If substrates other than bowl-shaped flowers provide better basking sites, then insects are unlikely to visit flowers for the sole purpose of basking.

Muscid, calliphorid, and syrphid flies commonly visit flowers of the alpine buttercup, *Ranunculus adoneus* Gray, an herbaceous perennial with heliotropic, yellow flowers. In June and July 1991, in alpine meadows (≈3,500 m elevation) on Niwot Ridge, Boulder County, Colorado (40° 3′ N, 105° 36′ W), I measured temperatures inside *Ranunculus* flowers and air temperatures immediately outside flowers using a bare, unblackened thermocouple. For 24 flowers, 1 thermocouple was placed inside the flower, the other thermocouple outside, and the temperatures of both were recorded every 30 s for 10–15 min. Average temperatures (for 10–15 min) were calculated for thermocouples placed in buttercups and for thermocouples suspended outside the flowers. These measurements allowed me to determine the degree to which temperatures inside these flowers were elevated. All temperature measurements were taken between 0900 and 1500 on clear, calm, cloudless days using a 2-channel electronic thermometer (Omega instruments model HH–25TC, Stamford, CT) with 40-gauge copper constantan thermocouples. Because of constant shifts in wind direction, attempts to perform these measurements during a variety of wind conditions were unsuccessful; given

Table 1. Thermocoupled fly measurements at a *R. adoneus* flower Niwot Ridge, 25 June 1991

Time, min	Temp of thermocoupled fly	
	Placed inside flower	Suspended outside flower
1	28.50	
2		28.10
3	30.60	
4		24.70
5	27.40	
6		25.10
7	27.10	
8		25.00
9	28.00	
10		25.70
11	31.00	
12		25.90
13	28.80	
14		28.00
Avg	28.77	26.07

the available equipment, accurate temperatures were obtainable only on days that were effectively windless at the ground surface.

Although the heat reward hypothesis was originally based on temperature measurements taken inside flowers using bare, blackened thermocouples (Hocking and Sharplin 1965), such measurements address only potential thermal benefits for insects visiting warm flowers, whereas the use of insects implanted with thermocouples provides a direct method for approximating actual benefits (Kevan 1975). To determine whether or not bare, unblackened thermocouple measurements closely approximate thermal benefits to basking insects, I compared measurements taken using bare thermocouples with measurements taken by holding anesthetized, thermocoupled flies inside and immediately outside flowers. To determine the magnitude of actual basking benefits to insects, 40-gauge copper-constantan thermocouples were implanted in the thoracic muscles of freshly captured and anesthetized (using ethyl acetate) calliphorid flies of the genus *Acronesia.* I placed a thermocoupled fly in an alpine buttercup as if it were basking, allowed it 1 min to come to thermal equilibrium (experimentation showed that 1 min allows the insect ample time to reach thermal equilibrium) and took its thoracic temperature. I then suspended the fly in the air at the same height (still within the boundary layer) as the flower, allowed it a minute to reach a stable temperature and took its temperature again. Average temperatures (10–15 min) were calculated for flies basking in buttercups and for flies suspended outside the flowers.

Because insects are black body objects and should gain heat when basking anywhere, thoracic temperatures of flies suspended in air provide a baseline measurement of the benefits flies obtain solely from basking anywhere in direct sunlight under calm conditions. Measurements of flower temperature indicate the potential benefits to insects of basking in flowers, but thoracic temperature measurements of flies placed in basking sites indicate actual benefits.

Table 2. Mean temperature ± SD for basking flies

Location	*n*	Temp°C
Plain thermocouple		
Outside flower	24	18.66 ± 3.24
Inside flower	24	24.21 ± 3.19
Thermocoupled fly		
Outside flower	22	23.19 ± 2.72
Inside flower	22	26.65 ± 2.78
Above ground	28	23.27 ± 3.03
On rock	28	29.54 ± 4.45

Individual flies were sometimes used for several thermocoupled fly observation periods. *n*, Number of different observations; average temperatures are for 10- to 15-min periods within each observation.

To determine whether flies derive greater benefit from basking in warm flowers or from basking on the ground surface (which consisted of loose, tan soil and slightly darker rocks), I evaluated the performance of flies basking on the ground surface. I used the same method as for flies placed in flowers. I placed a thermocoupled fly on the ground, allowed it a minute to equilibrate, and took its temperature. Next, I suspended the fly ≈5–10 cm above the rock (approximately the height of *R. adoneus* flowers), allowed it time to equilibrate, and took its temperature. Average temperatures (10–15 min) were calculated for flies basking on the ground surface and for flies suspended above the surface.

Results

A typical series of observations for a flower is included in Table 1, and summaries of results are included in Tables 2 and 3. Because data were taken in pairwise fashion, nonparametric pairwise statistics were used for the analysis. Bare thermocouples were warmer when placed inside flowers than when suspended outside (Wilcoxon 1-tailed signed ranks test, $T = 0$, $P < 0.01$), as were thermocoupled flies (Wilcoxon 1-tailed signed ranks test, $T = 0$, $P < 0.01$). Thermocoupled flies were warmer when placed on rocks than when suspended above rocks (Wilcoxon 1-tailed signed ranks test, $T = 0$, $P < 0.01$). Although temperatures measured with bare thermocouples were 5.26°C warmer inside flowers than outside the flowers ($n = 24$, 5.26 ± 1.16 [mean ± SD]), thermocoupled flies were only 3.46°C warmer when placed inside flowers than when suspended outside ($n = 22$, 3.46 ± 1.36 [mean ± SD]). Thus, measurements taken with bare thermocouples overestimated the basking rewards available to insects visiting flowers because insects gained a smaller amount of heat by basking in flowers than would be predicted from plain thermocouple measurements (Smirnov

Table 3. Temperature comparisons in various locations

Comparison	Test	n	T	P
Plain thermocouple in flower[a] vs outside	Wilcoxon	24	0	<0.01
Thermocoupled fly in flower[a] vs outside	Wilcoxon	22	0	<0.01
Thermocoupled fly on rock[a] vs in air	Wilcoxon	28	0	<0.01
Net thermal gain of bare thermocouple in *R. adoneus* vs net gain of thermocoupled fly in *R. adoneus*	Smirnov	24, 22	0.655	<0.01
Net thermal gain of fly in *R. adoneus* vs fly on rock[a]	Smirnov	22, 28	0.614	<0.01

[a] Warmer location. Temperatures are listed in Table 2.

test, $n = 22, 24$; $T_1 = 0.655$, $P < 0.01$). Thermocoupled flies placed on the ground, however, were 6.41°C warmer than flies suspended in air ($n = 28$, mean $= 6.41 \pm 2.40$ [mean ± SD]), and the ground was thus superior to flowers as a basking site (Smirnov test, $n = 22, 28$; $T_1 = 0.614$, $P < 0.01$). Results are summarized in Table 3.

Discussion

Because it appears that the best basking sites are on the ground, insects seeking heat alone are not likely to impose strong selective pressures for floral heat rewards. The primary benefit to plants of maintaining warm flowers could be direct; elevated flower temperatures could help offset growth and metabolic costs of reproductive structures (Kjellberg et al. 1982, Kevan 1989, Mølgaard 1989, Stanton and Galen 1989, Galen and Stanton 1991, Corbett et al. 1992, Galen et al. 1993). Although pollinators may have little reason to seek flowers as basking sites, pollinator-imposed selection may promote the maintenance of warm flowers. Any pollinator behavior that discriminates among flowers on the basis of temperature (for example, perhaps flying insects are more likely to visit flowers providing both food and warmth than those providing food alone) could result in higher quality pollination and consequent fitness benefits for heliotropic or warm flowers. Thus, although the evidence presented in this article suggests that elevated flower temperatures cannot be explained solely in terms of pollination, as long as there is a net thermal gain available to insects visiting flowers, it would be premature to dismiss this phenomenon as unimportant to the adaptations of alpine plants and their insect pollinators.

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References Cited

Corbett, A. L., P. G. Kraunitz, and L. W. Aarsen. 1992. The influence of petals on reproductive success in the arctic poppy (*Papaver radicatum*). Can. J. Bot. 70: 200–204.

Galen, C. and M. L. Stanton. 1991. Consequences of emergence phenology for reproductive success in *Ranunculus adoneus* (Ranunculaceae). Am. J. Bot. 78: 978–978.

Galen, C., T. E. Dawson, and M. L. Stanton. 1993. Carpels as leaves: meeting the carbon cost of reproduction in an alpine buttercup. Oecologia (Berl.) 95: 187–193.

Heinrich, B. 1975. Energetics of pollination. Ann. Rev. Ecol. Syst. 6: 139–170.

1979. Bumblebee economics. Harvard University Press, Cambridge, MA.

1993. The hot-blooded insects: strategies and mechanisms of thermoregulation. Harvard University Press, Cambridge, MA.

Heinrich, B. and P. H. Raven. 1972. Energetics and pollination ecology. Science (Washington, DC) 176: 597–602.

Hocking, B. 1968. Insect–flower relationships in the high Arctic with special reference to nectar. Oikos 19: 359–388.

Hocking, B. and C. D. Sharplin. 1965. Flower basking by Arctic insects. Nature (Lond.) 206: 215.

Kevan, P. G. 1972. Heliotropism in some Arctic flowers. Can. Field Nat. 86: 41–44.

1975. Sun-tracking solar furnaces in high Arctic flowers: significance for pollination and insects. Science (Washington, DC) 189: 723–726.

1989. Thermoregulation in Arctic insects and flowers: adaptation and co-adaptation in behaviour, anatomy, and physiology, pp. 747–752. *In* J. B. Mercer [ed.], Proceedings, International Symposium on Thermal Physiology, 16–21 July 1989, Troms, Norway. Elsevier, Amsterdam.

Kevan, P. G. and J. D. Shorthouse. 1970. Behavioral thermoregulation by high Arctic butterflies. Arctic 23: 268–279.

Kjellberg, B., S. Karlsson, and I. Kerstensson. 1982. Effects of heliotropic movements of flowers of *Dryas octopetala* L. on gynoecium temperature and seed development. Oecologia (Berl.) 54: 10–13.

Mølgaard, P. 1989. Temperature relations of yellow and white flowered *Papaver radicatum* in north Greenland. Arct. Alp. Res. 21: 83–90.

Morgan, K. R. and B. Heinrich. 1987. Temperature regulation in bee- and wasp-mimicking Syrphid flies. J. Exp. Biol. 133: 59–71.

Ring, R. A. and D. Tesar. 1981. Adaptations to cold in Canadian Arctic insects. Cryobiology 18: 199–211.

Smith, A. P. 1975. Insect pollination and heliotropism in *Oritrophium limnophilum* (Compositae) of the Andean Páramo. Biotropica 7: 284–286.

Stanton, M. L. and C. Galen. 1989. Consequences of flower heliotropism for reproduction in an alpine buttercup (*Ranunculus adoneus*). Oecologia (Berl.) 78: 477–485.

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