



Lizards as a plant's 'hired help': letting pollinators in and seeds out

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It is well-known that plants utilize many different kinds of animals for pollination and dispersal of their seeds, but an alternative kind of evolutionary relationship has attracted less attention: animals can facilitate pollen and seed transport without acting as a vector. We studied interactions between an epacridaceous plant (the honey bush, *Richea scoparia*) and a lizard (the snow skink, *Niveoscincus microlepidotus*) near the summit of Mount Wellington, Tasmania. The lizards gain access to the plant's nectar by tearing the fused petals (the calyptra) from the flower, thus exposing the plant's reproductive organs. Snow skinks forage selectively on flowers with higher-than-average nectar content, suggesting that this behaviour has evolved in response to plant characteristics. Lizard foraging may benefit *R. scoparia*, because calyptra remain attached unless a lizard tears the flower open. Our experiments demonstrated that the lizard's calyptra removal dramatically increased the plant's seed release. In 60 fruits from flowers with their calyptra intact, no seeds at all were released. However, 57 out of 60 (87%) fruits from flowers with their calyptra removed by the lizards successfully released their seeds. This system appears to involve reciprocal evolutionary changes in the interacting species (behaviour in the lizards and reproductive morphology in the plant). Thus the system seems to provide an unusual case of coevolution.

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ADDITIONAL KEY WORDS:—Lizard foraging – pollination and seed setting – coevolution.

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INTRODUCTION

“...I can understand how a flower and a bee might slowly become, either simultaneously or one after the other, modified and adapted in the most perfect manner to each other . . .” (Darwin, 1871).

In the years since Darwin's original insight, extensive evidence has accumulated on the ways in which reciprocal interactions between species can give rise to complex coevolutionary responses (e.g. Thompson, 1982, 1986, 1989, 1994; Endler, 1995). Some of the best examples of coevolutionary phenomena involve plant-animal interaction (e.g. Feinsinger, 1983; Ridley, 1996). As far as we are aware, however, there are no published reports of coevolutionary systems between plants and reptiles. This is despite reports of nectivory in many different lizard taxa and a significant role for lizards in pollination and seed dispersal (e.g. anoles, gekkonids, lacertids, scincids: Elvers, 1977; Valido & Nogales, 1994; Eifler, 1995; Font & Ferrer, 1995; Pérez-Mellado & Casas, 1997; Perry, 1997; Traveset & Sáez, 1997).

Features of plants that facilitate pollination or seed dispersal can involve many different kinds of traits. We report a rather unusual case, where the putative coevolutionary interaction involves a lizard that expedites pollination and seed release by physically removing the calyptra (= fused petal caps) that cover the reproductive parts of the plant. Hence, the plant ‘uses’ the lizard not as a pollinator, but as a mechanism to remove the calyptra at the optimal time for access to biotic and abiotic pollen vectors and, subsequently, for seed release. Such a system is likely to enhance plant fitness in an environment where the timing of calyptra release is crucial, and where alternative cues for calyptra release are poor predictors of suitable conditions for pollination. Our study system fulfils these conditions.

METHODS

Study area

Across Tasmania, the large island southeast of the Australian continent, montane areas are characterized by cool and windy conditions for most of the year. From 1992 to 1997, we studied lizards and plants in one such area: near the summit of Mt Wellington at 1270 m above sea level, 20 km S Hobart city. The study site is situated above the tree line, and consists of bare dolerite rock interspersed with hardy vegetation. The climate at this site is characterized by strong gusty winds and low temperatures with snow falling at any time of year (Fig. 1).

Study species

The Tasmanian snow skink (*Niveoscincus microlepidotus*) is a small (to 5 g, to 70 mm, snout-vent length) high-elevation specialist endemic to the southern part of Tasmania. The lizards are remarkably numerous on Mt Wellington; we captured >1500 lizards within an area of 50 × 50 m over the study period. One of the dominant plants in this area is the honey *Richea* bush (*Richea scoparia*), which is sympatric with *N. microlepidotus*, both species being confined to mountain tops throughout Tasmania

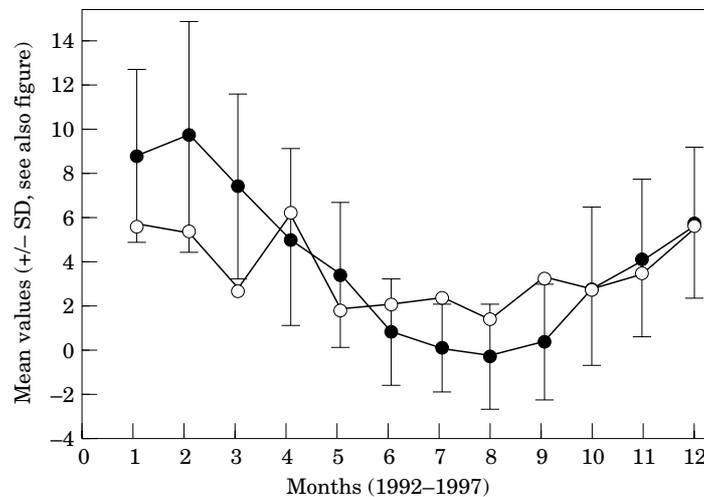


Figure 1. Climate data for Mt Wellington (monthly means of temperatures (●; °C) and precipitation (○; mm)) based on data recorded over the course of the study.

(Curtis, 1963; Cogger, 1996). The honey *Richea* (maximum height *c.* 1 m, maximum diameter *c.* 1 m at our study site) exhibits a perennial life history, although the same bush never flowers two years in succession. The flowers of *R. scoparia* form a terminal spike-like inflorescence (4–12 cm high; Curtis, 1963) organized in up to 20 whorls (=layers; Fig. 2). Within each flower the petals form a calyptrium (=cap of fused petals).

For most of the year, snow skinks are relatively unselective (predominantly insectivorous) predators, as most other small lizards studied to date (Avery, 1966; Rose, 1976; Huey & Pianka, 1983; Losos & Greene, 1988; Durtsche, 1992; Roughgarden, 1995), including other *Niveoscincus* species (Wapstra & Swain, 1996). During the flowering season of *R. scoparia* (December–March), however, snow skinks forage intensively on *R. scoparia* plants. Once a lizard selects a flower, it seizes the calyptrium and tears it off, thereby exposing the reproductive parts of the plant. The calyptrium containing most of the nectar is then chewed by the lizard, and the nectar extruded during the process is immediately consumed.

Adult snow skinks are large enough to forage anywhere along the inflorescence by reaching up on their hind legs, even on the largest inflorescences. If the lizards have evolved foraging behaviours that maximize their rate of nectar harvesting on the bushes, we would expect to see that the lizards select those flowers from the inflorescences that contain the most nectar. To test this prediction we gathered information on the distribution of nectar among flowers, and on the selection of flowers by lizards. To quantify nectar content, we collected inflorescences and scored the colour of the calyptria as either red (immature) or brown (mature) in the season 1993–94. A calyptrium from each whorl (Fig. 2) was selected haphazardly, removed with a pair of forceps, and squeezed from top to bottom between the thumb and the index finger. The nectar drop expelled from the calyptrium and any remaining droplet(s) on the reproductive parts of the flower was collected in a capillary tube of known volume, enabling us to calculate the nectar volume of each flower. Thus, we quantified differences in nectar volume among individual plants, inflorescences

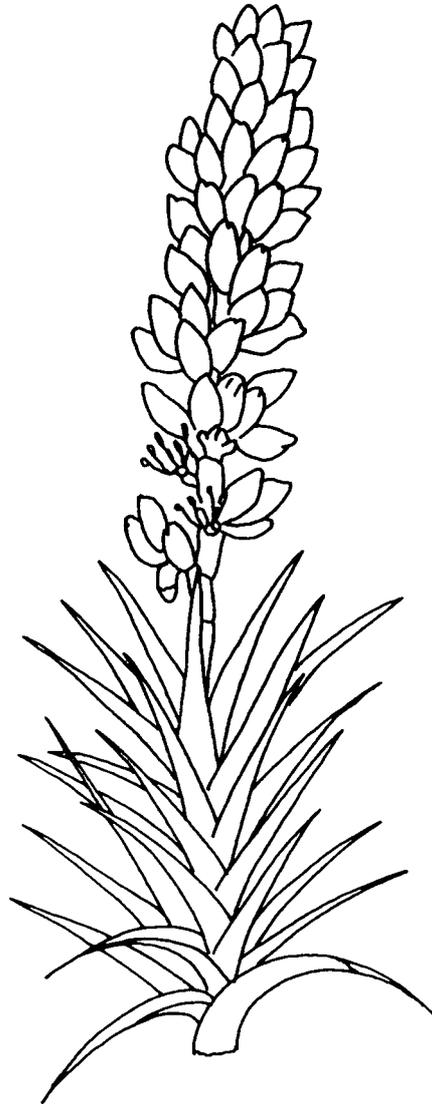


Figure 2. Inflorescence structure in the honey Richea, *Richea scoparia*, $2.0\times$ life size, depicting the positions of whorls of intact calytera (except for two of the lower ones) on an inflorescence.

within a single plant (range *c.* 10–several hundreds per plant), and among the whorls within each inflorescence (Fig. 2). We did not screen the chemical composition of the nectar. When drying, however, the nectar became highly viscous and sticky and, hence, appeared to have a high carbohydrate content.

We first monitored foraging behaviour of individual lizards in December 1993–January 94 by scoring the heights on the inflorescences (below vs above its mid whorl) at which the lizards foraged. All monitoring was done on days with sunny weather, at which the lizards can thermoregulate to their preferred body temperature (30°C , Jane Melville, pers. comm.). In order to determine whether lizards forage selectively with respect to calyptra position within each inflorescence (i.e. with respect

to height), we monitored the first and the second calyptrum that 19 adult skinks picked for nectar feeding on six different plants. To control for effects of calyptra colour (and hence flower maturation) we used bushes with >90% of the remaining inflorescences having entirely brown calyptra. While doing this, it also became apparent to us that inflorescences mature in a consistent fashion (from bottom to top), and that the time of maturation is consistent among adjacent flowers in a whorl. During this maturation process the nectar content of the calyptra increases in synchrony with its change in colour from pink/red to brown (King & Burns, 1969). This made it possible to increase substantially our data set on selective lizard foraging indirectly by photographing 11 well-separated plants (>15 m apart), incorporating the home ranges of several hundred lizards. To provide sufficient time for flowers to mature and for lizards to forage, we allowed at least ten days of good weather to elapse between our first and second photograph of each bush (first photo on 7 January, the second photo session was started 17 January but was interrupted by rain and therefore completed 26 January, 1997). From these photographs, we scored visitation rates on a total of 182 inflorescences (4–29 per plant). The first series of photographs was taken when calyptra were red (immature) with flowers containing little (if any) nectar and the second series of photographs when some of the flowers had matured (brown calyptra) and nectar contents were relatively high. By comparing the two photographs, we could score whether or not flowers had been visited by lizards (evidenced by removal of calyptra). To ensure accuracy in this assignment, we restricted our analyses to cases where the inflorescences consisted entirely of red calyptra from bottom-to-top in both the first and second photograph, or where all calyptra in an inflorescence had changed from red in the first photograph to brown in the second.

The potential benefit to the lizard of removing *R. scoparia* calyptra is obvious, since it provides the skink with fluid and carbohydrates. However, the more interesting question is whether or not the lizard's foraging behaviour has any consequences for the fitness of the plant. In order to investigate this possibility, we conducted a set of field experiments in which we excluded lizards from some of the bushes. To do this we covered parts of the plants with either coarse or fine netting (mesh sizes of 15 mm ($N=8$) or 3 mm ($N=9$), respectively). The coarse mesh allowed the lizards free access to the plants and hence provided us with a control, whereas the fine mesh prevented entry. At the end of the flowering season (February–March 1997), we haphazardly collected two inflorescences from the plants of the two experimental treatments (i.e. plants that were covered with coarse vs fine netting). The inflorescences were brought back to the laboratory, where we scored the number of flowers from which calyptra had or had not been removed.

A potential benefit to the plant of calyptra removal is a reduction in costs associated with inbreeding caused by selfing. Ideally, we would evaluate potential selfing costs by comparing the germination rate of seeds generated by out-crossing vs selfing. However, we have not been able to do this, in spite of initiating extensive germination experiments in collaboration with horticulturists specializing in Tasmanian plants ('Plants of Tasmania Nursery', Ridgeway, Tasmania); seeds of *R. scoparia* are notoriously difficult to germinate in the laboratory (Menadue & Crowdon, 1983). Instead, we looked at the number of seeds produced from flowers with their calyptra intact vs. removed (i.e. with vs. without the possibility of out-crossing). Seed release from the *R. scoparia* fruits in the wild took place in warm dry weather as a result of desiccation. We mimicked this process by keeping the fruits

TABLE 1. Nested analysis of variance in nectar content (df model = 39, df error = 442, $F_{\text{model}} = 8.99$, $P = 0.0001$).

Trait	Type I SS	MS	F	P
Plant	248.8	17.8	13.1	0.0001
Inflorescence (Plant)	227.8	9.1	6.7	0.0001

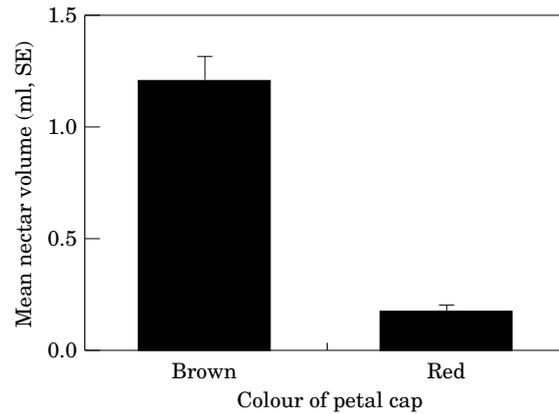


Figure 3. The calyptra of *Richea scoparia* change colour from red or pink to brown as they mature, and the brown flowers contain much more nectar.

in a well-ventilated room kept at 25°C, and scored whether fruits from the two categories of flowers (with vs. without intact calyptra) differed in the number of seeds they produced and in their capacity to release their seeds (within 2 weeks of desiccation). In the fruits that failed to open, the seeds were dissected out and counted under a stereoscope.

Tests for the statistical analysis are presented in association with their test statistics in the Results section. When data did not conform to normality, non-parametric tests were used.

RESULTS

Nectar content of calyptra and lizard foraging behaviour

We scored the nectar content of 484 calyptra from 45 inflorescences on 15 different plants. The nectar content of calyptra showed significant spatial variation at each level that we investigated: among plants and among inflorescences within each plant (Table 1). Nectar content also varied with the position of a calyptrum within an inflorescence: brown calyptra in lower than in higher positions contained more nectar (Fig. 4; nectar volume vs. whorl, Spearman's rank-order correlation analysis, $r_s = -0.31$, $P = 0.0001$, $N = 484$). Also, there was a seven-fold difference in average nectar content between red and brown calyptra (Fig. 3; t -test, $t = 8.3$, $P =$

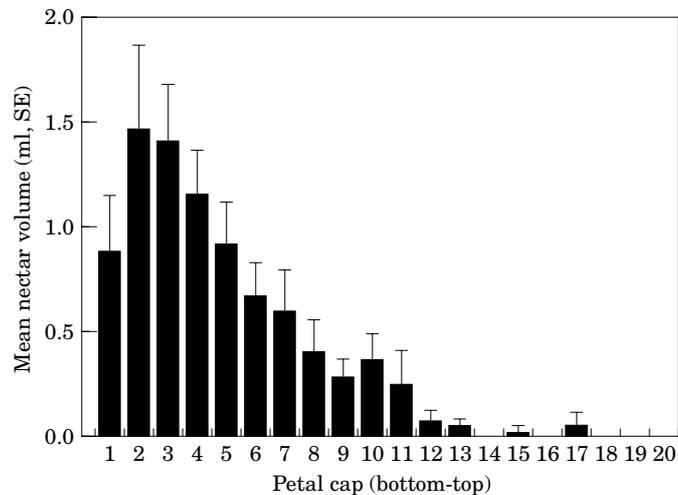


Figure 4. The nectar content of *Richea scoparia* calyptra varies with their position on the inflorescence (numbered on the x-axis from bottom to top); lower flowers contain more nectar.

0.0001). Thus, under the assumption that the lizards feed selectively on calyptra with high nectar content, we would predict most lizard visits to brown calyptra and/or calyptra positioned low on the inflorescence (Fig. 4).

In all our focal observations of foraging lizards, only brown calyptra were considered. Thus, there is no confounding effect of flower colour/phenology on the choice of flowers from different heights of the inflorescence. In 16 out of 19 cases, the first calyptra selected by a lizard came from the bottom half of the inflorescence. This result enables rejection of the null hypothesis that a selected calyptra was equally likely to have come from the bottom and top half of the inflorescence (binomial test, $P=0.004$). Twelve of these lizards went on to pick a second flower on the same inflorescence. Nine of these calyptra were again from the bottom half of the inflorescence. Although in the predicted direction, this latter bias is not statistically different from a null model of equal visitation rate of the bottom and top halves (binomial test, $P=0.07$). Thus, even in situations where calyptra colour (or the maturation process that it represents) is not associated with calyptra position, the lizards foraged non-randomly with respect to calyptra position, in such a way that they selected flowers with a high nectar content.

In our photographic comparison, inflorescences carrying calyptra that were still red in the second photograph had only been visited by lizards in two cases out of 17 (12%), whereas inflorescences that changed from red to brown were visited in 100 cases out of 125 (80%). The difference in visitation rate was thus highly statistically significant (Fig. 5; Fisher's exact test, $P=0.0001$). Under the assumption that inflorescences that changed from red to brown had been attractive to lizards for less time than inflorescences that were brown in both photographs, one would expect the latter category to have more lizard visits. The result was not statistically significant (Fisher's exact test, $P=0.30$) but in the predicted direction (80% vs. 90%; Fig. 5).

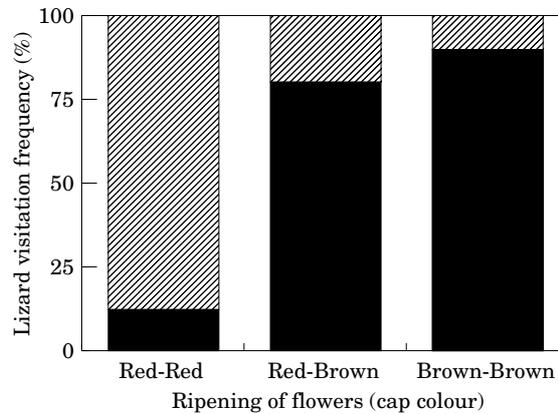


Figure 5. The frequency with which snow skinks (*Niveoscincus microlepidotus*) fed upon *Richea scoparia* flowers of different colours: (▨) not visited; (■) visited. The label on the horizontal axis refers to the calyptra at two times; when first photographed (7 January 1997) and when re-photographed at a later time (17 or 26 January 1997, the photography could not be completed 17 January due to rain). Thus ‘red-red’ calyptra were red at both times, whereas ‘red-brown’ flowers had changed colour during the intervening period. The skinks actively selected brown flowers.

Are the lizards responsible for the removal of the calyptra?

Direct observations show that foraging lizards remove the calyptra. However, it remains possible that the calyptra are released even in the absence of lizards, by strong winds. Our enclosure experiment was designed to assess this possibility. The result was clear cut: 96% of calyptra were removed from the flowers in the 36 inflorescences that were accessible to lizards (i.e. were ‘protected’ by coarse mesh that did not prevent lizard access), whereas only 16% were removed in the 36 inflorescences that were ‘protected’ by fine (‘lizard-proof’) mesh. The difference between the two treatments is too great to be attributed by chance (Wilcoxon two-sample tests, $Z=4.96$, $P=0.0001$). We conclude that lizards play an important role in calyptra removal for *R. scoparia* on Mt Wellington, much more so than does wind.

Does lizard foraging affect the fitness of the plant?

The removal of calyptra by the lizards could affect the fitness of the plant in at least four ways: (i) by transfer of pollen on the lizard’s head or other body parts, (ii) by facilitating pollination by other vectors (biotic or abiotic), through the exposure of the plant’s anthers and style; (iii) by facilitating out-crossing and thus reducing potential costs of inbreeding, and (iv) by facilitating the dispersal of seeds. We deal with each of these hypotheses below.

- (i) *Lizard pollination.* Detailed observations on nectar-foraging by lizards militate against this hypothesis. Lizards typically remove the calyptra, chew them from top to bottom, lick up the nectar drop and then spit the plant parts out. Hence, the lizard’s head and body rarely comes into contact with the anthers or style. We never observed pollen being carried by the lizard, and stereoscopic

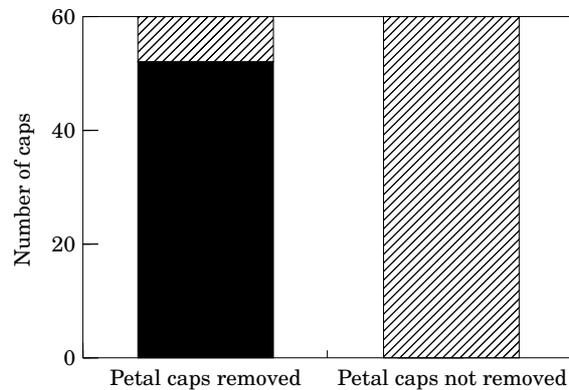


Figure 6. In the laboratory, *Richea scoparia* flowers with intact calyptra never released seeds (▨), whereas seed release (■) was much higher from flowers from which the calyptra had been removed by foraging lizards.

examination of moist cotton buds swabbed over the lizard's head and front part of the body revealed no instances of pollen transport.

- (ii) *Lizard calyptra removal followed by insect or wind pollination.* Wasps, dipterans, bumblebees and other several unidentified taxa of insect pollinators were observed feeding daily from the *R. scoparia* flowers that were made accessible by having their calyptra removed by the lizards. These observations support the notion that calyptra removal by the lizards is often followed by visits from potential insect pollinators. This is the only way that *R. scoparia* could out-cross, because intact calyptra prevent ingress of pollen.
- (iii) *Inbreeding avoidance.* Fruits from flowers with intact calyptra contained on average 116.8 seeds (± 47.6 , SD) and fruits from flowers with calyptra removed contained on average 122.6 seeds (± 31.5 , SD). The difference is not statistically significant ($t=0.50$, $P=0.61$, $df=48$). However, most of the seeds from fruits on flowers with intact calyptra were small and mouldy, unlike those on flowers where the calyptra had been removed, but we did not score these traits in greater detail.
- (iv) *Increased seed release due to cap removal.* Undoubtedly, an important fitness benefit to the plant of the removal of the calyptra by the lizards lies in increased seed release. Of 60 fruits from intact flowers, i.e. with their calyptra dried up, none opened to release their seeds. In contrast, seeds were released successfully from 52 out of 60 flowers (87%) with their calyptra removed (Fig. 6). This difference in seed release is highly significant ($X^2=91.8$, $P=0.001$ $df=1$). Furthermore, we never saw flowers with intact calyptra release their seeds in the wild. Thus, the calyptra have to be removed for seed to be successfully released. These results also suggest that selfing without subsequent removal of the calyptra would be fruitless in the literal sense of the word.

DISCUSSION

Several lizard species feed on nectar and other parts of flowers, and some of these lizards species play a significant role in pollen transfer (Pérez-Mellado & Casas,

1997; Traveset & Sáez, 1997) and seed dispersal (Valido & Nogales, 1994). We are, however, unaware of any previous example where a plant's reproduction (the dispersal phase, especially) appears to depend so strongly on a lizard. Our enclosure experiments show that *R. scoparia* is effectively unable to out-cross and has very poor seed release in the absence of lizards; this is further supported by the close geographic association of the two species. Which of the factors—pollination/out-crossing vs seed release—contribute the most to the plant's fitness? Our results do not allow us to rank their relative importance. Seed production, however, appeared to be unaffected by selfing. Indirectly, this argues against out-crossing benefits and similar lack of inbreeding effects on seed production has been described for other species (reviewed in Willson & Burley, 1983). Nevertheless, germination rate or seedling growth could still be influenced both by inbreeding and by what seemed to be an overall poorer quality of the seeds from selfing flowers. We were, however, unsuccessful at scoring germination rate in spite of several attempts to do so. Unfortunately, we never kept voucher seeds that could have been scored for viability using the tetrazolium test. In any case, such tests could not have demonstrated the post-germination fitness effects we were primarily interested in, such as differences in growth and, in particular, subsequent reproductive success between selfed and out-crossed zygotes. In conclusion, lizard foraging (i) *could* lead to out-crossing benefits that we have not been able to quantify, and (ii) *does* lead to markedly increased seed release.

How robust is our conclusion that the lizards are the most likely (if not the only) species capable of removing the calyptra and thereby allowing access to the flowers for visitors/pollinators? At this species-poor high altitude locality, there are few competitors for the flowers' nectar. The only birds in the study area are insectivorous and carnivorous species (scarlet robins, *Petroica multicolour*, and pied currawongs, *Strepera graculina*). Small nocturnal marsupials (e.g. *Antechinus swainsoni*) occur on the site, and have been implicated as nectar-feeders and pollinators in other areas (Watts, 1987). However, these animals would have been excluded from both our experimental treatments (because of their body sizes; Watts, 1987). Flying insects, such as wasps, many dipterans and the recently introduced bumblebee, *Bombus terrestris*, occur on the site, but are too small to pull off the calyptra. Instead, these insects obtain nectar by ingesting nectar droplets that may remain on the reproductive parts of the plant subsequent to a lizard visit, or by chewing a small hole at the base of the calyptra (bumblebees). This procedure does not increase the opportunities for out-crossing or facilitate seed release.

The ability of the lizards to select *R. scoparia* flowers with higher-than-average nectar content is interesting, especially in a reptilian lineage characterized by very general and relatively unselective insectivory. This supports the notion that the lizard-plant interaction that we have presented is a coevolved system (perhaps involving also other species of *Niveoscincus* although we have no evidence of this), where both species have been moulded by selection simultaneously or sequentially. The reliance of *R. scoparia* on foraging lizards for out-crossing and seed release is, however, more surprising and may be an adaptive response to the extreme weather conditions near the summit of Mt Wellington. If calyptra were released due entirely to a passive maturation process, it would be severely detrimental for pollination to the montane *R. scoparia* because the weather conditions at the mountain top are extremely harsh. In particular, very strong winds are the norm and the weather changes rapidly. In consequence, the activity schedule of lizards and insects coincide

with favourable weather for pollination (Fig. 1). Under these circumstances, the ‘strategy’ of linking calyptra release to lizard activity may provide a significant advantage and, hence, the *R. scoparia* plants on Mt Wellington appear to have evolved a reproductive system that depends upon the temporal correlation of activity times in two groups of ectotherms: lizards and flying insects.

The plants rely on a robust ectotherm (the lizard) for removal of the calyptra; it gives pollinators access to the open flowers, while ensuring subsequent seed release. Thus, the plants use ‘hired help’, paying with nectar for lizard labour.

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