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Explosive Pollen Release and Pollination in Flowering Plants

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Explosive pollination mechanism is one of the floral mechanisms that ensures successful pollination upon tripping by pollinating agents. The mechanism is found in several plant families, but widely frequented in Lamiaceae, Fabaceae, Loranthaceae, Rhizophoraceae and Onagraceae. The triggering agents of the explosive pollination mechanism in different families include flies, bees, butterflies, birds, bats and wind. The explosion of the pollination mechanism occurs by the violent movement of anthers/stamens style alone or together with restraining petals. The mechanism is basical in flag-blossoms and functional by sternotribic pollinators. The floral configuration in other explosive flowers varies but perfectly aligned for explosion. The explosive syndrome has been treated to be an adaptation for definite self and/or cross-pollination when triggered by the perfect pollinator(s).

Key Words: Explosive mechanism, Flowering plants, Bees, Birds, Non-explosion

Introduction

Flowering plants have developed various types of floral mechanisms as adaptations to their pollination syndromes. Explosive floral mechanism is one of such mechanisms that has been frequently reported in different genera falling in different angiospermic families such as Lamiaceae (see Aluri 1990), Fabaceae (Meeuse 1961), Loranthaceae (Feehan 1985), Onagraceae (Plitmann et al. 1973), Rhizophoraceae (Davey 1975, Tomlinson et al. 1979), Marantaceae (Davis 1987), Urticaceae (Taylor 1942), Ericaceae (Marie-Victorin 1942), Fumariaceae, Musaceae, Acanthaceae (Proctor & Yeo 1972), Cornaceae (Mosquin 1985), Orchidaceae, (Proctor & Yeo 1972, Gottsberger 1989), etc. Pollination in plants that possess the explosive or parallel mechanisms is a consequence of the violent movement of anthers/stamens and style alone or together with restraining petals (Aluri 1990). Such floral mechanisms ensure self/or cross-pollination when tripped by a legitimate forager by a slightest touch. The explosive mechanism is variously designed in different plant species and triggered by different species of insects and birds.

We attempt to put together the scattered reports in the literature that describe the plant species possessing the explosive or similar mechanisms. We also present the nature and function of these mechanisms in relation to pollination effected by tripping agents. Finally we discuss how the plants have developed the floral mechanisms independently in different families as warranted by the available vidence from the literature. This review forms a good source of information for extensive studies for a more clear understanding of independent or parallel development and evolution of explosive mechanisms in flowering plants.

Explosive Flowers and Pollination

We brief the available accounts of explosive pollen presentation as a function of flower-tripping by pollinating agents in different plant species (Family-wise).

Lamiaceae

The explosive pollen presentation is frequented in the subfamily Ocimoideae. The genus *Hyptis* in this subfamily is largely characterised by the explosive mechanism. Flowers of the members of this genus have the flag-shaped blossoms with the sexual organs always extending ventrally in the corolla tube, proximating to or along the lower flower lip, and not along the upper lip as in the majority of the Lamiaceae. The genus is characterised by sternotribic flowers in which the stamens are held in the lower lip of the corolla, which in majority of its species, is strongly compressed to form an explosive pollination mechanism (Harley 1971; 1976). In *H. suaveolens,* the floral carinal structure formed by the middle lobe of corolla lower lip conceals the stamens and stigma and does not open following the natural anthesis. Upon anthesis, the carinal lobe is tensed which is later released by wind or bees of various species. As a result, the stamens spring up, and eject a cloud of pollen upwards from the anthers. At the same time, the lower lip flips back and remain in that state permanently. The pollinators trip the explosive floral mechanism effectively in a single foraging visit resulting in pollen release from the stamens and subsequent pollen deposition on the stigma and on the forager in sternotribic manner. Wind trips the flowers to some extent and subjected to certain speed (Aluri & Subba Reddi 1989; Aluri 1990). *H. capitata* also has similar explosive mechanism but pollination is nototribic as the principle pollinating agent (wasp) collects nectar in such a way that the pollen is deposited on its dorsal side (Keller & Armbruster 1989). The explosive pollen presentation also occurs in *H. pauliana, H. emoryi, H. paradisi, H. siphonantha, H. alata, H. subrosea H. mutabilis, H. fasciculata, H. tagetifolia, H. hamatidens, H. peduncularis, H. nitidula, H. dictyodea, H. verticillata, H. pectinata, H. spicigera, H. atrorubens, H. brevipes, H. rhomboides, H. guanchezii,* etc. (Brantjes & De Vos 1981; Burkart 1937; Grant & Grant 1968; Harley 1974; 1983; 1989). Of these, *H. pauliana* and *H. subrosea* flowers are expected to be tripped by hummingbirds; *H. emoryi* by both hummingbirds and bees; *H. paradisi* and *H. siphonantha* by bees in sternotribic manner. The tripping agents for the remaining species are not known, but bees are expected to be their agents. The explosive mechanism occurs with slightest deviations in several allied genera such as *Aeollanthus* (Hedge 1972), Eriope (Harley 1971; 1976), *Marsipianthes, Peltodon Raphiodon* and *Homalocheilos* (Harley 1976).

A few species such as *H. cruciformis, H. pachyphylla* and *H. macrantha* have non-explosive floral mechanisms. In these, the lower lip is spoon-shaped and not held under tension by the stamens which are exposed as soon as the flowers open. With such a floral situation, the position of both anthers and stigma ensures contact with the foragers (bees) probing in an orthodox manner (Harley 1971; 1986). Similar non-explosive mechanisms occur in *Coleus* (see Faegri & van der Pijl 1979) and *Plectranthus* (Nilsson et al. 1985).

The explosive mechanisms are not found in other genera in the Lamiaceae that have been studied thus far. They have other types of floral mechanisms ensuring accomplishment of pollination when foraged by pollinating agents (Meeuse 1961; Proctor & Yeo 1972).

Fabaceae

Only a few species of this sub-family have developed explosion mechanisms in different forms and configurations. *Medicago sativa* and *Cytisus scoparius* have been widely reported in

the literature as best examples for explosive mechanism. *M. sativa* is the most important forage legume grown in North America (Childers & Barnes 1972) and is a perennial pasture and hay crop with an evolutionary adaptation for cross-pollination (McGregor 1976). Its flowers are pentamerous and zygomorphic; A large dorsal standard petal faces opposing wing petals, and a small pair of ventral keel petals encloses the sexual column so that it is held under tension. The pistil is surrounded by a column of nine fused stamens; a tenth free stamen arises from the receptacle of the flower just above the ovary base. The pressure exerted on the tensed stamen tube by a visiting bee causes the release of the stamen tube and the style explosively and the latter simultaneously strikes the underside of the visitor. The visitor in such an act is powdered underside with a cloud of pollen. Bees of *Nomia* and *Megachile* are credited with a major share in the pollination of this plant. Bees of *Apis* steal the nectar from the flowers through a side entrance and fail miserably to 'trip' the flowers. it appears that it almost as if honeybees have a strong dislike for getting a pollen cloud into their faces. Only accidentally, they trip a few flowers (Meeuse 1961).

C. scoparius has a similar mechanism but little more complicated. The keel and wings actually form one unit, the keel "hooked in" by a tooth on each side. The column of stamens, plus style, is for the time being kept in a straight position, but it is under terrific tension. The style awaits for the moment that it can pop out and curl up like a hoop. This movement arrives when a visiting bee alights and begins to push the keel down. The upper margins of the keel come farther and farther apart, the hidden column can no longer be kept in check, and all of a sudden the five short stamens pop out and powder the bee's underside with pollen. Immediately, the style and the long stamens curl around and strike the bee on the back of the abdomen. The visiting bee going from one flower to another causes explosion all over the place, the air is full of tiny pollen clouds resembling a scene full of gun smoke. The bees tripping the flowers are usually of *Bombus* and *Xylocopa* with large bodies (Meeuse 1961; Proctor and Yee 1972).

Ulex europaeus developed an explosive mechanism without offering nectar as reward to the visitor. In a flower, the two keel patals adhere lightly together by their upper edges; it is the keel that is held straight by the stamen tube and style, rather than vice-versa. The stamens dehisce just before the flower- opens. The flowers being nectarless are abundantly visited by bumblebees and honeybees which forcibly enter the flower as though seeking nectar. This action causes the keel petals to break apart, uncovering the stamens and style and bringing them sharply into contact with the insect, so dusting it with pollen on the underside of the abdomen. Once exploded, the spent flower hang limply open and is seldom visited again by bees (Proctor & Yeo 1972).

Spartium a plant that grows abundantly in the Mediterranean region has flowers that behave in exactly the same way as those of *C. scoparius* (Meeuse 1961). *Canavalia* is another plant having fabaceous floral structure with keel, wings and banner. However, the position of these petals is in striking contrast with its relatives. In nature, the flowers have a position with the banner down, not up. They are simply turned upside down imitating the flowers of Lamiaceae. The flowers are manipulated by bees of *Bombus* and *Xylocopa* receiving pollen on the back in much the same fashion as found in Lamiaceae members with similar floral structural arrangement (Meeuse 1961). *Mucuna* also has an explosive mechanism for the release of pollen. Its flowers are tripped and pollinated by bats (Vogel 1958).

Onagraceae

Lopezia is a small genus with 21 species adapted to pollination by hummingbirds and flies. Its

species are placed in six different sections because of their distinct varying floral characters (Plitmann et al. 1973). In the bird-pollinated species, *L. lopezioides* (section Diplandra), *L. semiandra* (section Riesenbachia), and *L. longiflora, L. grandiflora* and *L. langmaniae* (section Jehlia), the spoon-shaped staminode characteristically enfolds the anther of the fertile stamen in bud. The fertile stamen rotates by a twisting of the terminal, slender portion of the filament just before the flower opens. After the flower opens, the mature stamen sheds pollen upon visitation by birds. In consequence, the pollen in a mass by the viscine threads is snapped onto the back of the bird without explosion. After shedding pollen, the stamen is deflected farther downward, and the style grows outward to a position in which the tardily maturing stigma occupies the spatial relationship with the rest of the flower. On the contrary, all species of the section Lopezia are fly-pollinated. In these flowers, the rotated fertile anther is under tension by the enfolding staminode and snaps the pollen up onto the venter of any fly that alights and orients itself toward the pseudonectaries. The snapping phenomenon with or without explosion is not found in the species of sections Pelozia and Nannolopezia and *L. riesenbachia* (Eyde & Morgan 1973).

Rhizophoraceae

A wide range of distinct floral mechanisms has been found in this family. One of those mechanisms is explosive method of pollen release found in all species of *Bruguiera* and in *Ceriops tagal*. In these species, the stamens become enclosed in pairs by the petals, i.e., each petal functions as a pouch enclosing both an antepetalous and an antesepalous stamen. The latter is slightly lower in the flower than the former because of the basal twist in the filament. Tension is developed because the stamens press against the interlocked margins of the petals. When the flower expands the petal tends to bend back, but is retained in an erect position by the adherent ventral margins. Shortly before the flower opens the stamens dehisce. At anthesis, the sepals diverge presenting the closed, erect petals in the "cocked" position. Suitably triggered, the petal margins unzip instantaneously and fly apart, releasing the stamens which catapult the loose pollen towards the centre of the flower. In consequence, much of the pollen would be projected onto the head of an animal vector.

The mechanism for triggering a flower varies in different-sized flowers and according to the flower visitor. The flowers of large-flowered *Bruguiera* species such as *B. exaristata, B. gymnorrhiza,* and *B. sexangula* are tripped by birds of *Nectarinia, Meliphaga, Myzomela* and *Zosterops*. The small- flowered *B. parviflora, B. cylindrica* and *B. hainesii* are triggered by large butterflies. The delicate explosive mechanism in *C. tagal* is triggered by moth (Davey 1975; Tomlinson et al. 1979; Aluri unpubl. data).

The non-explosive mechanism is operative in *C. decandra* in which the petal-stamen configuration responsible for explosive- mechanism is lacking. The flowers are non-scented and visited by Trigonid bees. Similar non-explosive pollen release occurs in *Kandelia candel* (Tomlinson et al. 1979).

Loranthaceae

Explosive opening of flowers in this family was first described by Evans (1895) and was noted briefly by a number of field botanists (Johow 1900; Volkens 1899; Werth 1900; 1915; Winckler 1906). More detailed observations of Loranthaceae pollination mechanisms in particular species were recorded by Goebel (1920), Docters van Leeuwen (1931, 1954) and Vogel (1954). Feehan (1985) presented a review of explosive pollination mechanisms in Loranthaceae. The general flower of Loranthaceae is characterised by the following characters. The flowers are bisexual and dichlamydeous; calyx is generally

reduced to a vestigial calyculus. The erect corolla or yellow colours constitutes a deep nectar containing closed tube. In African genera the tops of the petals are variously spoonshaped and strengthened with horny tissue. This region of the petal is called the 'spathula' constituting a distinct head on the flower, often separated from the main corolla tube by a narrower collar. The explosive flowers are found in the genera.

Erianthemum species contain explosive mechanism tripped by sunbirds seeking nectar. The individual flower is a slender column, densely covered with long silky hairs, which tapers abruptly to a point at the top, and with a swelling at the base above the calyculus as the flower begins to mature. Later, the swelling becomes in orange colour and the strap-shaped petals separate and arch outwards in the region immediately above the orange zone. The openings between the petals are called the 'fenestrae'. The separation of the petals is an apparent result of differential growth in the stamens and this growth continues setting up tensions in the flower. If the flowers at this stage are visited by sunbirds, instantaneous explosion of flowers and subsequent pollination occurs. What actually happens is that the birds insert its beak through one of the fenestrae to imbibe the nectar at the base of the corolla, and as the beak is withdrawn its upper part comes into contact with the arch at the top of the fenestra. The pressure of the beak tears the petals apart. Then, the filaments all curve inwards like watch springs and the curling stamens dust the head of the visiting birds with pollen, and the style, released from its confinement in the corolla tower, curves forward - towards any pollen which may already be on the pollinator's head.

Englerina is a small genus characterised by brightly coloured flowers, match-like in form, with distinct head, collar, and corolla tube. Details of explosive pollination in *E. inaequilatera* and *E. heckmanniana* are available. In these species, a mature flower possesses fenestrae in the collar region below the match head-like apex, causing the separated petal segments in this region to arch outwards. The flower explodes when the beak of the sunbird is inserted between the two petals below the fenestra. Consequently, the stamens curve inwards in tight spirals, dusting the head of the pollinator, and the pistil curves slightly in the same direction.

Tapinanthus is a large genus containing species with fenestrae and without fenestrae. The explosion pollination mechanism in those species which have fenestrae is an elaboration of the elegant theme found at its simplest in *Englerina*. This kind of fenestral explosive mechanism occurs in *T. rufescens, T. eminii, T. sansibarensis, T. vittatus, T. guttatus* and *T. subulatus*. The non-fenestral species such as *T. sessilifolius, T. quinquangulus* and *T. guttatus* possess two-stage mechanism: the head produces a purple pigment in the spathulae which engages the attention of the pollinator. Probing of the flower head by the beak causes the spathulae to reflex backwards suddenly and completely, so that the style and stigma surrounded by a tight column of stamens project above the collar, into which the bird now inserts its beak to reach nectar in the corolla tube. The movement of beak causes the stamens instantaneously curl inwards into tight spirals, dusting the pollinator's head and bending the style with its capitate stigma forward in the same direction.

Globimetula species have an elaborated basic floral features that found in fenestral *Tapinanthus* species. The first stage in dehiscence is brought about by simple pressure on the head. The spathulae immediately reflex, and the segments of the corolla tube backwards. The first stage reveals a second tube inside the outer corolla tube enclosing the fused stamens which form a scarlet column around the style, and the stigma projecting through it. Half way down the anther column there are fenestra-like windows through which the nectar in the corolla tube can

be seen. When the pollinator's beak is inserted through one of these windows, the stamens curl inwards explosively, bending the style in the same direction.

Species of *Plicasepalaus* and *Vanwykia* have non-explosive mechanisms and the open flowers are regularly visited by sunbirds.

Marantaceae

Members of *Thalia* possess secondary pollen presentation by explosive mechanism. Prior to anthesis, pollen is deposited in a stylar depression behind the stigma. When the flower opens, the style is hidden by a cucullate staminode, held in tension by a pressure sensitive spur. If a bill of a bird or proboscis of a bee is inserted into the corolla and struck the spur with sufficient force, the style is catapulted around to the front of the flower, bringing the stigma in contact with the intruder, and simultaneously despositing pollen on the visitor. Such explosive pollen release and nature of pollination are found in *T. geniculata, T. dealbata* and *T. trichocalyx* (Kennedy 1978; Davis 1987).

Urticaceae

Urtica dioica has explosive pollination mechanism. This species has small unisexual flowers; male and female flowers occur on separate plants. The male flowers have four perianth segments and four stamens; the stamens are incurved and under tension in the bud, and spring back, scattering the pollen explosively into the air, after the flowers open. The mechanism is triggered by the pressure developed inside the flower and no external agent is involved in triggering the mechanism (Proctor & Yeo 1972). Similar explosive release of pollen into the air by rapid swinging of anthers has been found in *Pilea microphylla* (Taylor 1942).

Ericaceae

A simple note from Marie-Victorin (1942) indicates that *Kalmia angustifolia,* a member of this family has a sort of explosive manner of pollen release from the flowers. The anthers are partially embedded in the petals and are released at maturity with the petals playing a stationary role.

Fumariaceae

Corydalis lutea has an explosive mechanism reminiscent of that of *Medicago* or *Cytisus.* It has four petals of which the upper most is the largest and has a long spur at its base. The two lateral petals are curved inwards at their margins and fused at the tip, so that they form a sheath enclosing the rigid style. The stigma is large and lobed. The bumblebees which visit the flowers depress the hood as they probe for nectar in the spurred upper petal. Consequently, the bees dust themselves with pollen in the process. *Fumaria* species also have similar flowers to *Corydalis* (Proctor & Yeo 1972).

Musaceae

Proctor & Yeo (1972) document that *Ravenala madagascariensis* has an explosive mechanism but details regarding the mode of operation are lacking. *Strelitzia reginae* flowers have three outer orange segments which serve for display. Two of these segments conceal the stamens while the third conceals the ovary. The segments that conceal the stamens have lobes and facilitate the visiting birds to stand in order to reach the nectar. The weight of the bird pushes the lobes apart almost explosively so that the anthers are then exposed and dust the underside of the bird with pollen (Scott-Elliot 1891).

Cornaceae

The genus *Chamaepericlymenum* representing only two species is characterised by its unique explosive mechanism. A needle-like antenna situated at the tip of one of the four petals in *C canadense* flowers triggers the explosive mechanism instantaneously by a slightest touch. The petals would reflex, the anthers would spring out simultaneously like four tiny catapults and

shoots their entire pollen loads into the air above the inflorescence.

The principal tripping agents of this mechanism are *Megachile* bees (Mosquin 1985). An identical mechanism has been reported for *C. suecicum* (Marie-Victorin 1942).

Acanthaceae

Odontonema schomburgkianum has its flower-tube closed at the top until probed by a bird, when it opens explosively, scattering a cloud of pollen over the visitor (Proctor & Yeo 1972).

Orchidaceae

Listera ovata flowers have a lip broadly strap-shaped, bent sharply downwards from a point near its insertion, and deeply notched at the tip. It forms a landing place leading upto the column; a groove, secreting much nectar, runs up the centre of the lip from the notch at its tip. The anther lies behind the rostellum, protected by a broad expansion of the back of the column. The anther-cell dehisce before the bud opens, and the pollinia are left quite free, supported in front by the concave back of the rostellum. A visiting insect crawls slowly up the narrowing lip, feeding on the copious nectar, which leads it to a point just below the rostellum. On the gentlest touch the rostellum exudes, explosively, a drop of viscid liquid which, coming into contact with the tips of the pollinia and with the insect, cements them firmly to its head and sets in a matter of seconds. After the pollinia have been removed, the rostellum slowly straightens from its arched position close to the lip, leaving clear the way to the stigma. Now an insect crawling up the nectar groove can pollinate the flower with pollinia brought from another flower. An essentially similar mechanism is seen in *Neottia nidus-avis* (Proctor & Yeo 1972; see Gottsberger 1989).

Discussion and Conclusion

The review suggests that the explosive or parallel mechanisms occur in both temperate and tropical plant species. In tropics, the weather being dry and hot during most part of the year facilitate easy explosion of the flower upon a gentle touch by the pollinators. In strong contrast, the weather in temperates during major part of the year is humid and cool; and unfavourable for flower explosion. In consequence, the plants that have explosive flowers appear during summer and fall seasons when the weather is relatively warm and dry. The explosive pollination syndromes found in both temperate and tropical plant species have adapted to tripping by insects, principally bees, or birds.

In Lamiaceae, the explosive pollination syndrome is a characteristic of *Hyptis;* few other species in different genera have the mechanism but they can not be characterised as such in total. The explosive mechanism is adapted to tripping by bees, wasps and hummingbirds, and also by wind in case of *H. suaveolens* (Aluri 1990). The explosive flowers in Fabaceae, Fumariaceae, Cornaceae, Orchidaceae are adapted to tripping by bees; those in Musaceae and Loranthaceae by birds; those in Marantaceae and Acanthaceae by bees and birds; those in Onagraceae by hummingbirds and flies; those in Rhizophoraceae by birds, butterflies and moths; those in Urticaceae by wind. Some bees of *Bombus* and *Xylocopa* and birds of *Nectarinia* are capable of tripping, very efficiently, the explosive mechanism with different floral configurations and architectures that have been found in flowers of different species. Honeybees working on *Medicago* flowers have learned that by probing the keel from the side, they can get at the nectar more easily and avoid the discomfort of a sharp blow on the underside from every flower (Proctor & Yeo 1972). Syrphid flies working on *Chamaepericlymenum* flowers for pollen appear to have some threat to their life from the flower's needle-like antenna and pop- mechanism (Mosquin 1985).

In the subfamily Ocimoideae, the explosive pollen presentation seems frequent. The frequent occurrence of this mechanism does not necessarily imply a phylogenetic link between genera within the subfamily but suggests this might have evolved independently several times in the different genera. The development of explosive nature of floral mechanism might have been made possible by the dominance of the lower lip. The lip was probably of adaptive value as a landing place or stamen protector before the explosive mechanism evolved. Moreover, the position of the anthers in the lower lip in the bud is common to the whole subfamily. The position in the upper lip is phylogenetically and ontogenetically secondarily attained in connection with a change towards nototriby (van der Pijl 1972). Evidence for a phylogenetic origin of the explosion mechanisms comes from the diversity of associated structures (Hedge 1972). The conclusion is that the explosive mechanism in the Ocimoideae may have developed independently atleast twice by parallel evolution and may not indicate a common phylogenetic origin.

The papilionate flower relates to flag-blossom with the filaments united into a tube and primarily adapted to sternotribic pollination. With such a floral configuration, the flower makes the way clear for the forager. The only difference between ocimoid flower and papilionate flower in configuration is that the dorsal stamen is absent in the former and free in the latter to provide easy access to the nectar. Bees of different species are instrumental in administering the explosive tripping process. More case studies from Fabaceae are needed to view the origin and development of the explosive mechanism within the subfamily.

In Onagraceae, the only genus that has explosive flowers is Lopezieae with 21 species under different sections. Except for Nannolopezia and Pelozia, all other sections show explosive mechanism adapted to tripping by birds and flies. Plitmann et al. (1973) hypothesize that the snapping phenomenon here is evolved from the common ancestor of section Lopezia, and was a single, unique event. They indicate that section Pelozia was derived from its common ancestor with section Lopezia before the evolution of the snapping mechanism. The morphological variations in the floral parts of *Lopezia* species have been presented by them for convincing evidence for their hypothesis.

In Rhizophoraceae, *Bruguiera* is characteristically a representative of explosive mechanism. The only species outside this genus that has explosive flowers is *Ceriops tagal.* The large-flowered Bruguieras are adapted to tripping by birds, while the small-flowered ones by large butterflies. *C.tagal* is exclusively triggered by moths. The explosive mechanism in this family represents a considerable specialization and a monophyletic origin seems likely. *Ceriops* may be the key genus in this process since it includes both specialised and unspecialised taxa. Adaptive radiation leads to *Bruguiera* condition (Tomlinson et al. 1979).

Regarding Loranthaceae, there appears to be a close relation between Loranths and Nectarinids. Such a relation stresses a symbiotic relationship between them. Feehan (1985) suggests that pollination in *Erianthemum* can be effected by nectar-feeding birds of various families, while in genera like *Tapinanthus* and *Plicosepalus*, successful triggering of the pollination mechanism depends upon the size and shape of the bird's beak and its foraging behaviour. The floral evolution in loranths has probably been directed by the selective pressures exerted by nectariniid evolution and behaviour.

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