

Bud-opening by the Mason bee *Hoplitis* (*Hoplitis*) *perambigua* (Peters, 1975) (Megachilidae, Osmiinae) on Lanzarote, Canary Islands, Spain

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Zusammenfassung

Jacobi, B., Wood, T. J.: Knospenöffnen durch die Kanarische Natterkopfbiene *Hoplitis* (*Hoplitis*) *perambigua* (Peters, 1975) (Megachilidae, Osmiinae) auf Lanzarote, Kanarische Inseln, Spanien. In einer Population der Art *Hoplitis perambigua* auf Lanzarote wurden Weibchen regelmäßig beobachtet, wie sie unter kraftaufwändigem Anheben eines Corollarlobus in eine kurz vor dem Aufblühen stehende Knospe eines hermaphroditischen Individuums der Natterkopf-Art *Echium decaisnei* einschlüpften. Die Weibchen sammelten im Innern Pollen an den Antheren, deren Filamente noch stark gekrümmt sind und ihre endgültige Länge noch nicht erreicht haben. Möglicherweise werden die Theken dazu aktiv eröffnet. Eine Knospe enthält offenbar genug Pollen für eine Füllung der Scopa. Die Pollenernte ist auf diese Weise besonders ergiebig, da Konkurrenz durch andere Pollennutzer ausgeschlossen wird. Die Mortalität durch Epiphyten wird gleichzeitig minimiert durch den fast vollständigen Sichtschutz, den die Knospe der im Innern sammelnden Biene gewährt.

Resumen

Jacobi, B., Wood, T. J.: Apertura de capullos florales por la abeja silvestre *Hoplitis* (*Hoplitis*) *perambigua* (Peters, 1975) (Megachilidae, Osmiinae) en Lanzarote, Islas Canarias, España. Hembras de una pequeña población de la abeja silvestre *Hoplitis perambigua* en Lanzarote fueron observados penetrando capullos de la flor de una planta hermaphrodita de Taginaste *Echium decaisnei* para elevándose uno de los lóbulos cortos del cáliz bajo esfuerzo. Dentro el capullo de la flor las hembras colectaron polen especialmente efectivo. Puede ser ellas abren las thecas activamente. Un capullo de la flor aparentemente contenía suficiente polen por una carga completa. Probablemente en este manera la competencia con otros visitantes florales fue grandemente reducida. Además la abeja colectora esta protegida visualmente dentro el capullo de la flor, reduciendo el riesgo de predation.

Summary

Females of a small population of the mason bee *Hoplitis perambigua* on Lanzarote were observed forcefully entering pre-anthesis flowers of a hermaphrodite plant of the bugloss species *Echium decaisnei* by lifting one of the five still overlapping short corollar lobes. The females busied themselves for up to a minute inside the bud collecting pollen from the anthers of the still short and re-curved stamens. It is possible that the thecae are actively opened in the process. Pollen harvest was extremely effective in this manner, one flower bud apparently holding enough pollen for a full scopal load. Competition by other flower visitors must be substantially reduced or even entirely avoided. Additionally, the harvesting bee is almost completely hidden from view inside the bud, certainly minimizing the risk of predation.

Introduction

Taxonomic history of *Hoplitis* (*Hoplitis*) *perambigua* (Peters, 1975)

The species made its first appearance in literature in Lieftinck (1958) under the designation of '*Osmia spec. indet. aff. insularis*'. Peters (1975) recognized the form belonged to the *anthocopoides*-group in the subgenus *Hoplitis* Klug 1807, characterized by the large triangular to semicircular emargination of the hind margin of the male 6th sternite and described it as *Osmia anthocopoides perambigua*, acknowledging the similarity of the genitalia with those of *O. anthocopoides*. While Baez & Ortega (1978) listed both above designations, Hohmann & al. (1993) were the first to give species status to *Osmia* (*Hoplitis*) *perambigua*. Michener (2000, 2007) and Müller (2016, 2018) assign generic rank to *Hoplitis* and consequently we use *Hoplitis* (*Hoplitis*) *perambigua* (Peters, 1975) for the species treated here.

Distribution and Phenology

According to Hohmann & al. (1993), *H. perambigua* is endemic to the Canary islands and has been recorded on Lanzarote, Fuerteventura, and Tenerife. It should be

expected to be present on Gran Canaria, too. The above authors published records of *H. perambigua* for Fuerteventura covering the end of December through to April with most from February (with one additional record for September), for Lanzarote covering February and March (plus one additional record for April 1st), and for Tenerife from February, March, and April.

All our own observations were made January 1st - 4th 2019 and January 9th 2022 on Lanzarote (BJ) and March 6th 2015 on Tenerife (TJW).

Brief portrait of host plant *Echium decaisnei* Webb & Berth

Echium decaisnei is a woody perennial candelabra-shaped endemic of the Canary Islands recorded from the islands Fuerteventura and Lanzarote (ssp. *purpurens* Bramwell) and Gran Canaria (ssp. *decaisnei*). It is frequently planted as an ornamental shrub or honeybee forage in public green spaces, gardens or on farms well outside its natural range of steep slopes in northern Lanzarote and southern Fuerteventura. The species is gynodioecious like many other species of *Echium* (Camus 1937, Bramwell 1972, Dorken 2010), so there

are female plants (Fig. 1) with short stamens bearing sterile anthers and hermaphrodite plants with long stamens producing fertile pollen. The hermaphrodite individuals are proterandrous. When the rather sparse amount of pollen per flower is gone, the thecae wilt and shrivel and the style splits distally exposing two terminal globular stigmata. Because it is well known that gynodioecy enhances outbreeding, Böhle et al. (1996) suggested "that outbreeding is manifest among island inhabitants as the result of counterselection of inbreeding depression in selfing colonizers" (p. 11744).



Fig. 1: Female plant of *Echium decaisnei* (29.12.2018). Finca Lomos Altos, Macher, Lanzarote (photo: Jacobi)

Observations

Descriptions of nest site, nest substrate and nests

In a young 6 years old plantation of olive trees a single block of rust-coloured porous lava of roughly 30 x 30 x 25 cm used to weigh down an irrigation pipe was found to contain several nests (Fig. 2). This rock was very close to a healthy looking hermaphrodite plant of *Echium decaisnei*, no more than four meters distant. There were no similar promising nesting substrates close to the



Fig. 2: Lava block with nests of *Hoplitis perambigua*. Two ♀♀ are visible: one to the upper left resting in front of her nest and one lower middle inside her nest with only the hind end of metasoma exposed (3.1.2019) (photo: Jacobi).

other *Echium decaisnei* plants near, some of which were only just starting to flower, appearing drought-stressed and/or were female.

The small nests, likely single-celled, were difficult to spot, as colours exactly matched the surface of the nest rock. In depressions in the rock, caused by larger gas filled cavities in the lava laid open by later fracture, nests were made inside 'bubbles' accessible by irregularly formed orifices, created when a fracture missed the maximum diameter of the gas inclusion. Eclosion holes of 2–3 mm diameter were visible in old nests, from which offspring had already left. The irregular polygonal shape of these holes was likely caused by the removal of small angular pieces of lava from the cell wall, embedded in the ochre loamy mortar used by the nest building females in the previous season. Old nests were apparently being reused.

Male behaviour at nest site

Males were frequently seen resting for a few seconds on the single discovered nest site (Fig. 4). Occasionally they entered narrow holes in the same lava block (Fig. 3), that were not occupied by nesting females. Apparently these holes were used for spending nights, too. At times a male and a female were seen sitting on the lava block for a few seconds only a few centimetres apart without interaction. No mounting behaviour was observed. There were smaller as well as larger males, the largest matching the largest females. Occasionally a male, recognizable by the greyish eyes (black in females) and brown scutal pilosity (off-white in females), was seen inspecting the *Echium* flowers in flight or nectaring briefly.

Upon request the gardener placed another similarly sized but black lava rock at a similar distance to the plant observed opposite to the one already present. One hour later a male was seen sitting on the 'new' rock briefly. Several times a male was seen sitting on a black irrigation tube (bearing a blue longitudinal stripe) near the nest site.



Fig. 3: *Hoplitis perambigua*-♂ about to leave its over-night shelter. Note the greenish eyes. Obviously the hole has also been used as a retreat by a spider (4.1.2019) (photo: Jacobi).



Fig. 4: *Hoplitis perambigua*-♂ resting briefly near a nest from a previous season from which at least one bee has eclosed by dislodging an angular piece of 'picón' (photo: Jacobi).



Fig. 5: *Hoplitis perambigua*-♀ resting on the lava block containing nests. Note open mandibles and tongue folded back below the bee, touching the rock surface (3.1.2019) (photo: Jacobi).



Fig. 6: *Hoplitis perambigua*-♀ sitting below an open brood cell (belonging to a second female). The pictured female possibly intends to build a brood cell of her own within the small space she is straddling (04.1.2019). (photo: Jacobi).

Female behaviour at nests

When resting for a short time on the nest rock, females held their mandibles open and held their long tongue folded back, touching the rock below the head and thorax, exactly as *H. adunca* females do (Fig. 5).

Females were seen entering nests and working inside (Fig. 6). The exact nature of their doings could not be verified due to their small size. As least one female was observed leaving and returning at rather short intervals (ca. 20 seconds), these being much too brief for

acquiring a full pollen/nectar load. So possibly it was cleansing an old brood cell.

Sometimes a female sat in the entrance of her nest, head inside with movements suggesting it was fashioning the 'lip' of the nest.

On a single occasion two females were seen working very close to each other, one inside a future brood cell, the other on the outside of the nest where there was still room for another brood cell in the same small and rather shallow depression in the rock.

The first female was later seen provisioning the same brood cell in the way typical for Megachilidae bees: entering the cell head first to offload nectar, then backing out, turning round and entering in reverse to deposit pollen. The pollen visible in the scopa was a slightly buffish white, exactly matching the colour of *Echium decaisnei* pollen seen on dehiscent stamens.

Female behaviour at flowers

The species was observed exclusively on a single hermaphrodite individual of *Echium decaisnei* (Fig. 7–9). Several conspecific plants present on the same organic farm were either female or not yet flowering.

At this plant frequently up to half a dozen females were observed whizzing around the *Echium* inflorescences simultaneously. Their flight was swift, the course being changed frequently and erratically, so the bees were difficult to follow with the eye, especially with the black 'picón' [lava gravel] the farmer had evenly spread on top soil in the background.

Sometimes the bees (females and occasionally males) entered an open flower to take up some nectar, while bracing themselves with their mid-legs laterally in the comparatively wide corolla.

The females did not seem to be much interested in the many flowers already open, though, the majority of which were in female phase with hardly any pollen left on the stamens protruding from the corolla surrounding the now extended and receptive style. The length of the bees was insufficient to simultaneously touch the thecae at the distal end of the anthers and reach the nectar at the bottom of the corolla.

Occasionally a female was seen hugging the bunch of stamens protruding from a recently opened flower, working these with legs and mandibles, probably removing remaining pollen.

Occasionally a female landed on a flower bud and subsequently scrutinized it. While in some cases the female took to the air again soon, in other instances, on more progressed buds, the female was working hard to get her lower face under the rim of one of the topmost corollar lobes closing the unopened flower by overlapping considerably. This process, once started was not

aborted even at the close approach of the observer with a camera. It took the bee several seconds to bend up one petal-tip sufficiently to wedge in first the head, then the thorax and finally to enter the flower completely. The small opening did not shut again but rather widened by the movements of the bee inside. The lower parts of the bent back stamens were blocking the opening like 'bars in a jail window'. The female was seen using mandibles and forelegs to manipulate the anthers inside the flower, extracting pollen in the process, as additionally evidenced by the progressively filling ventral scopa.

No other bee species was observed locally collecting pollen on *Echium decaisnei*!

The dearth of honeybees was a puzzle, because four hives were standing less than 100 m from both *E. decaisnei* plants. Possibly this was the combined effect of several causes: the presence of *Philantus triangulum*, a couple of shrikes *Lanius meridionalis koenigi* feeding nestlings, the watery nectar of *E. decaisnei* flowers, presence of only a single hermaphrodite *E. decaisnei* plant and competition by the bud-burgling *Hoplitis perambigua*.



Fig. 7: *Hoplitis perambigua*-♀ nectaring from a female phase flower of a hermaphrodite *Echium decaisnei* plant. Note how she secures herself with the antero-laterally extended mid legs (2.1.2019) (photo: Jacobi).



Fig. 8: *Hoplitis perambigua*-♀ lifting the upper two corollar lobes of a flower bud of a hermaphrodite *Echium decaisnei* plant using her head (1.1.2019) (photo: Jacobi).



Fig. 9: *Hoplitis perambigua*-♀ harvesting pollen from the anthers still enclosed in the bud using her front legs and mandibles. Note the anthers' filaments are still bent back, barring easy access to the corolla (02.01.2019) (photo: Jacobi).



Fig. 10: *Hoplitis perambigua*-♀ offloading nectar into a brood cell she is provisioning. Note the scopa filled with pollen (4.1.2019) (photo: Jacobi).

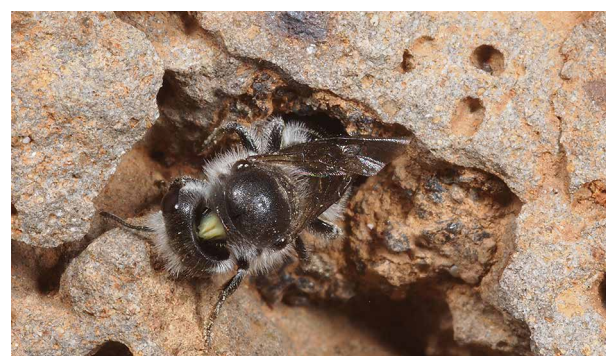


Fig. 11: The same female seconds later, entering her brood cell backwards to offload pollen from the scopa (4.1.2019) (photo: Jacobi).

Additional observation from Fuerteventura

Müller (in lit.) on April 2nd 2015 observed two *Hoplitis perambigua*-♀♀ collecting pollen from *Echium bonnetii* at Gran Valle (close to Barranco de Gran Valle) at approximately 100 m a.s.l.

Additional observations from Tenerife (TJW)

Hoplitis perambigua was observed on March 6th, 2015 in the hills above El Palmar, on the trail between the village of Teno and the viewpoint Mirador Altos de Ba-

racán in the north-western corner of Tenerife. The trail runs along the south side of the hill crest and is consequently in a rain shadow, with laurel forest on the north facing slope and scrubland on the south facing slope. This scrubland is interspersed with small boulders. On closer inspection, the boulders contain many small crevices that a number of *Hoplitis perambigua* females were entering (Fig. 12). The bees moved around the boulder very close to the surface even when flying, making netting them in flight challenging. Unfortunately only a single female was collected, and this specimen carried no pollen. The identity of the yellow pollen grains scattered across the surface of the rock in [Figure] are unknown. There was very little in flower in the surrounding scrubland apart from occasional patches of *Euphorbia* and *Echium*. To the north in the laurel forest there were many stands of *Echium* sp. in flower, but the only bee species recorded visiting was *Amegilla canifrons*.

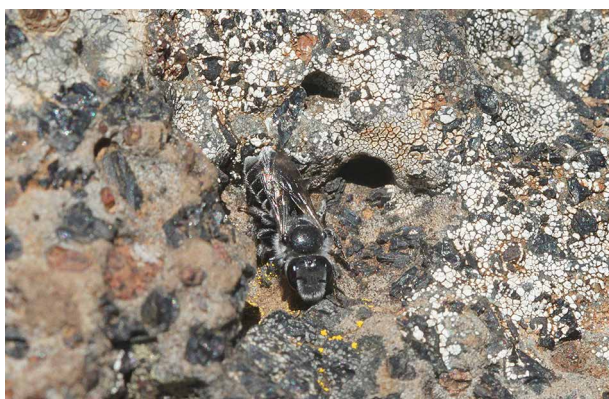


Fig. 12: *Hoplitis perambigua*-♀ resting on a rock probably containing nests, El Palmar, Teno, Tenerife (6.3.2015) (photo: Wood).

Discussion

Bud-opening and related phenomena

To be the first to enter a male-phase flower is highly rewarding for pollen collecting bees. To achieve this, the bee either must be present exactly when the flower opens or force entry into the pre-anthesis flower-bud with or without damaging the flower. In the case reported here no damage apparently is done to the corolla, but possibly the thecae are actively opened.

Hurd & Linsley (1963) reported on *Perdita hurdi* (Panurginae) entering pre-anthesis flower buds of *Proboscidea arenaria* via a small hole cut with the mandibles to collect pollen. While in this case pollination most likely is accomplished by the females visiting open flowers of the same species for nectar afterwards, in another case reported by Jacobi & Newmann (2012), two species of Australian native solitary bees use their toothed man-

dibles to cut open flowers and then use their fore tarsi equipped with spatulate bristles to extract pollen from pre-anthesis flowers of *Grevillea* spp. In these cases, individual flowers are damaged to a greater or lesser extent and the contribution to pollination by the visiting bees is probably negligible.

Inouye (1980) reviewed the pre-1980s literature on "illegitimate" flower visitations (visits not effecting pollination) and the terminology that has been used therein, but does not include the study by Hurd & Linsley. Most of the types of "larceny" (Inouye's term) relate to accessing nectar and are not of central interest here. Inouye (1980) discriminates two types of larceny aimed at pollen removal: pollen theft (removal without force) from anthers or stigmatic surfaces and pollen robbing (removal with application of destructive force).

Social bees of genus *Trigona* were reported by Renner (1983) to cause massive destruction to a majority of flowers of individual Melanostomataceae plants in South America by cutting into the anthers and extracting pollen more or less completely.

Wall & al. (2002) reported on a case of flower manipulation of flower buds by a bee leading to premature anthesis in Florida, USA. A close parallel was reported by Newman & Jacobi (2011) on 'cap-lifting' in several Australian species of solitary native bees removing the opercula of pre-anthesis flowers of a *Eucalyptus* species to gain first access to the pollen.

There are obvious parallels between these cases and the one here discussed, as time is invested and force is applied to access the full pollen content of a pre-anthesis flower, without noticeable damage to the flower. Saunders (2017) reported on *Hylaeus perhumilis* collecting pollen from stamens of *Corymbia ficifolia* that had not yet become erect soon after the operculum was shed normally. Even if this stage might be called pre-anthesis in the broadest sense, the behaviour does not qualify for bud-opening.

Batley (2019) documented bud-opening behaviour in seven species of Australian native bees. In the case involving *Lasioglossum* (*Chilalictus*) *eremian* opening buds of *Eremophila sturtii*, the buds are opened in a manner very similar to the case reported here, i.e. by forcing upward a corollar lobe to gain access to the anthers.

Müller (in lit.) found bud-opening quite common among European native bees of several families: *Lasioglossum convexiusculum* and *L. xanthopus* on *Salvia*, *Andrena lathyri* on *Vicia*, *Andrena chrysopus* on *Asparagus*, *Osmia pilicornis* on *Pulmonaria* and many more.

For *H. anthocopoides* Eickwort (1973) observed "... both males and females repeatedly investigated nearly open

buds [of *Echium vulgare*] and even occasionally gnawed at them." [p. 13], a possible starting point from evolutionary perspective to the development of bud-opening. Perhaps most bees are equipped with enough behavioural flexibility and learning capacity to individually 'invent' this strategy?

Morphological adaptation for bud-burglary?

As females were observed to use mandibles and fore-legs to free/extract pollen from the closed/partially opened thecae, we looked for anatomical adaptation(s) on the front tarsi, which might have been evolved for increased efficiency of pollen harvest inside buds, but did not detect anything conclusive. Whether or not some unspectacular small pads of short hair on the inner side of the front tarsal members 3 and 4 could qualify as adaptive we are unable to decide.



Fig. 13: *Hoplitis perambigua*-♀ in lateral view with tongue extended. Legit 6.3.2015 & in coll. (photo: Wood).



Fig. 14: The same *Hoplitis perambigua*-♀ in frontal view (photo: Wood).

Narrow oligolecty on *Echium* most likely

Sedivy & al. (2013) constructed a DNA-based phylogeny of the *Annosmia-Hoplitis*-group and concluded: "Both parsimony mapping and maximum likelihood

inference of ancestral states clearly suggest that the ancestor of the *Annosmia-Hoplitis*-group was oligolectic on Boraginaceae..." [p.10]

According to Sedivy & al., within *Hoplitis* (s. l.), several lineages of that group have independently switched to use other plant families as pollen hosts, most commonly to the family Fabaceae (possibly via a polylectic phase).

Hohmann & al. (1993) list names of 10 plant species from six families visited by *H. perambigua* when captured. Females of the species have been encountered on six species of four families: *Chrysanthemum coronarium* and *Launea arborescens* (Asteraceae), *Echium lancerottense* and *E. plantagineum* (Boraginaceae), *Euphorbia obtusifolia* (Euphorbiaceae) and *Lotus lancerottensis* (Fabaceae). Pollen collection was recorded on none of these plants.

Eickwort (1973) in his detailed study of the biology of *H. anthocopoides* (studied in New York State, this species being adventive in North America) wrote: "It seems reasonable to propose that the evolutionary progenitor of *Hoplitis* s.s. was a species that was a successful specialist in using *Echium* flowers..." [p.26]

Peters (1975), recognizing the close affinity of *H. perambigua* to *H. anthocopoides* assumed *Echium* oligolecty for the latter, too.

Based on the similar morphology of the male sternites, Müller (in lit.) confirmed the close relationship of *H. perambigua* to the proven narrow *Echium* oligolectes *H. anthocopoides* and *H. lepeletieri* in agreement with Peters (1975).

During prolonged observations of flowering *Lotus lancerottensis* stands on Lanzarote and Fuerteventura on occasion of several travels by BJ, not a single *H. perambigua* was recorded among the flower visitors.

Including observations detailed above assuming narrow oligolecty on *Echium* for *H. perambigua* seems most likely.

Flowers of genera other than *Echium* probably are visited for nectar only.

Effectiveness of *H. perambigua* as a pollinator of its host plant

The pollination efficiency of *H. perambigua* is expected to be rather low. Applying the bud-opening technique observed, the females visit flowers in their early male phase to collect pollen. They visit female phase flowers on the same plant, too, but just for nectar. By being shorter than the corolla length, the bees are unlikely to touch the stigma for pollen deposition and thus probably do not contribute significantly to pollination. The same would apply if a female plant grows near, which might also be visited for nectar, but if the small size of

the bee would correlate with a smaller average flight range, probability of visits to female plants is expected to decline steeply with distance. Pollination effectiveness may increase slightly under optimal growing conditions for the host *Echium decaisnei* in natural setting on north-east facing steep slopes, allowing for low inter-individual distance between members of a large host population. Larsson (2005) found females of an oligolectic bee, *Andrena hattorfiana* to be the single most effective transmitter of pollen to stigmata in the host *Knautia arvensis* owing to their high percentage of all flower visits, but all other non-specialist visitors combined (including the males of *A. hattorfiana*) were collectively far more effective. So in the case reported here, the females of *Hoplitis perambigua* are likely to be only suboptimal pollinators, i.e. depositing less pollen on stigmata per visit than a non-specialist visitor. From the perspective of the host *Echium decaisnei*, the polylectic *Anthophora alluaudi* is almost certainly a more effective pollinator given its larger size, hairier body, and expected greater foraging range. *Anthophora alluaudi* has been observed by BJ systematically working inflorescences of female as well as hermaphrodite *E. decaisnei* for extracting nectar. Handling time per flower was about a second and the hovering or briefly sitting bee always touched the bifid stigma and anthers, if present.

Now that four *Echium* species are known to be used by *H. perambigua* in Lanzarote and Fuerteventura, it would be interesting to know, which of the nine species of *Echium* from Tenerife are used as pollen hosts. For *Echium simplex*, growing in the Anaga region of Tenerife, Jaca & al. (2018) found "Flying insects, especially bees, were the most frequent pollinators and the most effective, i. e. those contributing most to the reproductive success of *E. simplex*." (p. 9).

Jaca & al. (2018) did not find *Hoplitis perambigua* among the flower visitors of *E. simplex*, although the former is present in the Anaga region on Tenerife according to Hohmann & al. (1993), where the study of Jaca & al. (2018) was conducted.

Additionally, Valido & al. (2019) also did not encounter *H. perambigua* visiting *Echium wildpretii* inflorescences (see below under 'Distribution').

Size and colour of *H. perambigua*

The smaller size of the species (compared to larger relatives) reduces the amount of pollen needed to produce a single offspring.

Additionally small size reduces attractiveness to predators, like insectivorous birds. In flight a small insect must be less visible than a larger one. This can be hypothesised to be advantageous during the prolonged

phases of search for buds about to open observed.

Small size also allows for passing between the strong filaments of the stamens, blocking entrance to any larger insect in the closed flower.

Due to the larger surface to volume ratio small insects do not retain body warmth well, but for the same reason absorption of sun-radiation will heat up a small black insect faster than a larger one, reducing basking time and thus predation risk. The flight musculature works best when sufficiently warm so rapid flight can be sustained, which combined with erratic manoeuvres again decreases visibility as well as predictability and consequently lowers the risk of predation.

In a semi-desert environment, black integument in a day-flying insect seems counter-intuitive. Camouflage on dark rocks and against the glassy jet black lava picón might compensate a possible disadvantage.

Type of nest

From the limited observations from two of three volcanic islands it appears, *H. perambigua* prefers to nest in small cavities in porous lava blocks and uses rather limited amounts of masonry.

The related *H. anthocopoides* from continental Europe builds aggregated brood cells on rock faces, usually in some slight depression. These are later covered by a continuous layer of mortar. The co-occurring commoner and larger *H. adunca* makes use of deeper cavities, usually in rocks or walls but also in wood, offering more protection especially laterally.

In the absence of a ecologically similar related competitor the small *H. perambigua* can choose freely among an over-abundance of available preformed cavities. So nests of *H. perambigua* are in a way intermediate between those of *H. adunca* and *H. anthocopoides*.

Distance nest - pollen host

Even though the maximum recorded migration distance of a marked female of the close relative *Hoplitis anthocopoides* (adventive in North America) reported by Eickwort (1973) is 640 m, the average distance covered between nest and pollen host is much smaller.

Blank & Rothe (1999) reported distances of 0 - 5 (-20) m between nests and host plant stands in *H. anthocopoides* in eastern Germany.

The average nest-host distance may be even less in the smaller *H. perambigua*, given the windy conditions found the semi-desertic island of Lanzarote, devoid of higher vegetation to break the wind. This limitation might additionally explain why the bee was found only on one host plant, which had a suitable nesting rock within a few meters distance.

Distribution of *H. perambigua* and hints on its biogeographical history

Hoplitis perambigua apparently has a disjunct distribution on Tenerife in two areas which have much in common: Anaga and Teno. Both are the remnants of much older previously separate islands united only later by vast eruptions that formed the central, largest and highest part of Tenerife (including Las Cañadas and Teide) as it is now. Teno as well as Anaga has relics of laurel forests from the Tertiary period, which are absent from the younger central part of the island. So *H. perambigua* is known from the oldest islands (ca. 20 million years old) in the archipelago and on the older parts of Tenerife which were formed in a later episode of volcanism (ca. 14 my).

A close relationship to *H. anthocopoides* as suggested by Peters (1975) would exclude a colonization of the Canary islands in sync with the progressive formation of volcanic islands increasingly distant from the north-west African mainland. Close relationship rather points to a more recent colonization from north-western Africa, first to Lanzarote and Fuerteventura and then to Tenerife.

So far *H. perambigua* has not been found on Gran Canaria and Gomera, which were formed roughly at the same time with Tenerife, nor on the younger and higher parts of the latter. Additional searches are necessary to have confidence that the species is genuinely absent.

The apparent absence from the central part of Tenerife may simply reflect unsuitable conditions.

Not surprisingly Valido & al. (2019, in 'supplementary information') did not encounter *H. perambigua* in Las Cañadas del Teide, Tenerife, where the gigantic *Echium wildpretii* grows. The height of 2000 m a.s.l. well exceeds the altitudinal range of *H. perambigua* as presented by Hohmann & al. (1993) which extends from sea level to just below 1000 m.

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