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An observation of active flight in *Pachycerus* Schönherr: Can macropterous weevils be flightless? (Lixinae: Cleonini)

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Abstract. Flight in the Cleonini genus *Pachycerus* is reported for the first time. As the Cleonini where thought to be flightless in the past, and information on the capability to fly can be difficult to obtain, further lines of evidence are discussed. Are long wings and well developed flight muscles sufficient to assume the ability to fly? The hypothesis that such a species is able to fly cannot be falsified: A lack of observations could just indicate the rarity of the phenomenon. Conversely, the ability to fly can only be proven by direct observation. Thus, the importance to publish any observation of flight is highlighted.

Keywords. Flightlessness, flight muscles, Curculionidae, wing dimorphism, flight dimorphism,

Introduction

As flight is crucial to colonize new habitats in a fragmented landscape, the flight ability of an insect has far reaching implications for systematics, biogeography, conservation and crop protection. Therefore, the questions how often, how far and where insects of economical importance or conservation value fly, have been frequently discussed in scientific literature (e.g. Stein 1972, Dubois & Vignon 2008, Hedin et al. 2008, Chiari et al. 2013, Drag & Cizek 2018). However, such detailed information is not available for the majority of weevils.

Despite possessing long wings and well-developed flight muscles, many beetles, including weevils, have never been observed to fly (Smith 1964). It remains unclear whether these morphological traits translate into actual flight capability. This discrepancy raises an intriguing question in entomology: Do species that morphologically appear capable of flight always fly?

Flight in lixine weevils

The curculionid subfamily Lixinae is composed of the tribes Lixini, Cleonini and the species-poor Rhinocyllini (Meregalli 2014), but there is evidence that those tribes are not monophyletic (Volovnik et al. 2021). In contrast to the Lixini, some of which fly not only for the purpose of dispersal but also to escape disturbances, flight is rarely observed in the Cleonini. Anderson (1988) wrote about the Nearctic species that "adults of most species of traditional Cleonini are brachypterous and even those that are macropterous have not been observed to fly."

Due to the scarcity of published flight observations in the Cleonini, these are often overlooked. Consequently, it has been proposed that the entire tribe, including macropterous species, is flightless (Arzanov & Grebennikov 2017). According to Meregalli (2014), most Cleonini have functional hind wings, but many genera are brachypterous or wingless (with some genera, among them *Pachycerus*, having winged as well as brachypterous or apterous species). Volovnik et al. (2021) were able to report flight in seven species, citing published accounts as well as recent observations:

Asproparthenis punctiventris (Germar, 1823) Bothynoderes affinis (Schrank, 1781) Cleonis pigra (Scopoli, 1763) cf. Conorhynchus conirostris (Gebler, 1829) Cyphocleonus dealbatus (Gmelin, 1790) Eurycleonus talamellii Meregalli, 2005 Temnorhinus brevirostris (Gyllenhal, 1834)

Korotyaev et al. (2020) also disagree with the claim that all Cleonini are flightless. They note the exceptional rarity of published flight observations of *Asproparthenis punctiventris* (Germar, 1823) (Cleonini) in comparison to *Lixus subtilis* Boheman, 1835 (Lixini). Both species have been studied in detail, as they can damage sugar beet plantations.

A very thorough work on the biology of *A. punctiventris* was published by Tielecke (1952), focusing on aspects relevant to crop protection. Sugar beet is usually cultivated in crop rotation. Each generation has to migrate, as they will not find many suitable host plants growing on the field in the year they emerge. According to Tielecke's own observations and the sources he cited, the beetles are usually migrating by foot, but can fly (even in masses) when the air temperature is exceeding +22 °C and the sun is shining. He was not able to induce flight in the laboratory, where he simulated temperature but not sunlight.

For *Pachycerus*, no unambiguous references of active flight observations have been found in the literature. Huber & Vayssières (1990) tried to rear specimens of an unidentified *Pachycerus* from Iran, and reported that specimens where "attempting to fly when placed in direct sunlight", but that "adults were never seen flying in nature".

Observed flight in Pachycerus Schönherr

A flying specimen of *Pachycerus* cf. *segnis* was observed on May 11, 2021 by nature photographer Frank Leo in the South of Brandenburg (Germany), at the "NABU-Naturparadies Grünhaus". The area is a former open-pit lignite mine between Finsterwalde, Senftenberg and Lauchhammer. Pictures (Fig. 1) were taken immediately after the specimen had landed, when the hind wings where still unfolded.

The exact identification of the specimen is impossible at the moment due to taxonomic uncertainties in the genus (Meregalli 2013). The palearctic species of *Pachycerus* are in need of revision. As recent material suitable for DNA extraction is scarce in collections, it would be highly appreciated if specimen are preserved in ethanol to contribute to a revision including molecular data in the future. The habitat preference as well as the life cycle of *Pachycerus* in Brandenburg was described by Esser (2013).

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Fig. 1. The specimen of Pachycerus cf. segnis after landing, the hind wings are still unfolded. Image: Leo/fokus-natur.de

Discussion

Can species with macropterous individuals be entirely flightless? These observations are giving rise to the question of whether all long winged species of Cleonini have the capability of flight, even if it has never been observed.

Flight in insects is strongly influenced by wing length, flight muscle development and behaviour. While some species are uniform, many exhibit intraspecific polymorphisms of these characters, so that flying, intermediate and non-flying individuals can be distinguished within the same species or population. Such polymorphisms have been discussed thoroughly, for example by Harrison (1980), Den Boer et al. (1980), and Thayer (1992). This is very important, as it means that findings from observations of a few specimens cannot be applied to the species as a whole, as the proportion of flying vs non-flying individuals may vary between populations. Intraspecific polymorphism of the hind wing and the corresponding musculature is well known in Curculionoidea (e.g. Oberprieler et al. 2014, Stein 1968). Korotyaev et al. (2020) report a wing length polymorphism in *Maximus strabus* (Gyllenhal, 1834), but otherwise the occurrence of flight polymorphisms in the Cleonini is not well documented.

The formation and upkeep of long wings and the corresponding muscles are resource-intensive, which would hypothetically induce the evolutionary trend to reduce those features if they are not being used. This would allow for the assumption that at least some individuals can fly if long-winged individuals are found within a population.

However, there is some evidence indicating that exceptions may exist. Smith (1964) stated about beetles that "It is well known [...] that many species, though winged, are never seen in flight.". It remains unclear whether such species would turn out to be flying upon closer examination (like the Cleonini), or if truly flightless species with well-developed hind wings do exist.

A well-studied example outside of Coleoptera could be the supposedly flightless firebug, *Pyrrhocoris apterus* (Linnaeus, 1758). Socha & Šula (2006) report that long wings and developed flight muscles are retained in some individuals, even though they cannot fly.

The flightlessness of macropterous individuals of *P. apterus* has been supported experimentally (Socha & Zemek 2000), but it has to be noted that it is impossible to prove the absence of a potentially rare phenomenon with certainty. There is the possibility that flight behaviour is triggered by certain conditions which aren't easy to simulate in an experimental set up. This is always to be considered when a species is called "flightless". Actually, there is at least one published flight observation of *Pyrrhocoris apterus*, which remained unnoticed by Socha & Šula (2006) and Socha & Zemek (2000): Seidenstuecker (1953) was able to induce flight in macropterous individuals in the laboratory. After several unsuccessful attempts, he succeeded when he provided suitable structures for take-off and raised the temperature to +40 °C. Such temperatures are not typically reached daily in the natural environment of *P. apterus*, which may have contributed to the absence of other published records of flight in this well-known species.

If long wings and flight muscles would be retained but not used, either they would have some benefits apart from flight, or their resource cost is not high enough to select towards reduction. The existence of flight polymorphisms suggests that the features that are required to fly are resource-intensive, so that they are reduced whenever possible. However, it could be argued that the most important evolutionary driver in those cases is not resource cost, but the ability to fly itself. For example in ground beetles it is well documented that the number of short-winged individuals is higher in populations on islands or in fragmented landscapes. This is because the flying genotype is constantly being removed from the population (Den Boer et al. 1980). If flight muscles and long wings have other benefits than flight, they could be retained even if the ability to fly has been lost. In the aforementioned case of Pyrrhocoris apterus, Socha & Šula (2006) have hypothesized that flight muscles are beneficial as a resource deposit, which can be histolyzed to allocate resources for reproduction.

"Phenological Flightlessness"

In many insect species a dispersal phase, after which the ability to fly is lost, takes place before reproduction (Harrison 1980). As flight muscles make up a significant proportion of their body mass, it is common among female insects to reduce them after a short dispersal phase, to reallocate resources to egg production (Roff 1990). The trade-off between flight and reproduction has been dubbed the "oogenesis-flight syndrome" (Johnson 1969).

While there is no common pattern for all species, some beetles may use their flight muscles to migrate into suitable hibernation sites, reduce them during winter to save energy, regenerate them in spring before they migrate by flight into reproduction habitats and degenerate them for reproduction (van Huizen 1977, Muda et al. 1981, Lebenzon et al. 2022). It is known that some species of bark beetles (Curculionidae: Scolytinae) regenerate their flight muscles after reproduction to do a second dispersal flight (Jones et al. 2019).

Whether "phenological flightlessness" is occuring in the Cleonini has apparently not been studied in detail yet. Literature on *Asproparthenis punctiventris* is suggesting that they fly after hibernation to find suitable host plants (e.g. Tielecke 1952, Drmić et al. 2019). There are more papers on seasonal flight patterns in other Curculionoids (e.g. Stein 1972, Muda et al. 1981), suggesting that it is a common trait.

Conclusion

It can be assumed that in most species where long-winged individuals have been recorded, at least a small proportion of individuals are able to fly at some point in their life. However, there is the possibility that flights are extremely rare even in individuals which can fly. The existence of flightlessness in individuals with fully developed hind wings and flight muscles would be hard to prove for methodological reasons. In fact, it is a hypothesis which cannot be falsified unless flight is observed. The only certain way to prove flight capability is through direct observation. Flight can be difficult to induce in an experimental set up, thus it is important that anecdotal observations are published.

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