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RESPONSE

Response to Packard (2025): Energetic costs of large weapons could constrain their size in large male stag beetles *Cyclommatus mniszechi*

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Packard's letter entitled 'Reconsidering mandibular and metabolic allometries in males of the stag beetle *Cyclommatus mniszechi* (Coleoptera, Lucanidae)' (Packard, 2025) contends that we arrived at incorrect allometric conclusions in Chen et al. (2024) by examining data on the logarithmic instead of the arithmetic scale. Packard has made this point repeatedly in comments on studies of allometry (e.g. Packard, 2023 and references therein), blaming conservatism for the continued use of log-transformed data. Many biologists disagree (e.g. Tsuboi, 2019 and references therein) and point out that models need to consider the theoretical context of allometry rather than just statistical fit (Tsuboi, 2019), that biological processes are 'multiplicative by nature' and best represented logarithmically (Kirkhoff & Enquist, 2009) and that the log-transformed methodology is preferable because Packard's approach hinders biological interpretation of the parameters (Lemaître et al., 2015). This argument will clearly not be resolved in this commentary. We, however, would like to point out that Packard's assertions (Packard, 2025) about the conclusions of Chen et al. (2024) are unfounded and misleading.

Energetically costly weaponry

As is clear from its title ('Energetically costly weaponry in the large morph of male stag beetles'), our principal objective in Chen et al. (2024) was to investigate whether the energetic costs of large weapons might constrain their size in large individuals. To do this, we examined how the standard metabolic rate (SMR) of 52 male and 35 female beetles related firstly to their body weight (fig. 2, Chen et al., 2024) and secondly to a combination of their body size and weapon size (fig. 3, Chen et al., 2024). We show that SMR increases disproportionately with both body weight and the body size/weapon size combination, and that weapon size only helps determine SMR significantly in the largest (major) males.

Packard partly reproduces and reworks the first of these models, excluding the females. He derives a single curve (fig. 2c, Packard, 2025) through the arithmetic male data rather than two lines through the ln-transformed male data. But his own graphs (fig. 2) show the same increased metabolic cost of large body weight as ours. Contrary to his statement, adopting his curve would in no way have altered our conclusions.

As it did not include the females or model weapon/body size against SMR, Packard's (2025) analysis does not confirm or contradict the conclusion that large weapons contribute significantly to SMR only in large (major) males.

Male dimorphism

Dividing the males into different morphs was not a principal focus of Chen et al. (2024); it simply adopted the minor and major morphs developed and justified in Chen et al. (2020). To evaluate whether the males could be divided into different morphs based on the allometric relationship between body and weapon size, Chen et al. (2020) measured the morphological traits of a larger sample of males (n = 232 rather than 52 males in Chen et al. (2024)). It is, therefore, misleading for Packard (2025) to imply that Chen et al. (2024) divided the males into two morphs based on the traits of the 52 males.

Chen et al. (2020 and references therein) discussed the beetles' morphology in some detail – males of the species had previously been classified into alpha, beta and gamma morphs based on the size and shape of their mandibles, including differences in the tusk-like projections (denticles) in their distal half. Chen et al. (2020) followed Knell (2009) in considering non-linear allometries and evaluated the fit of various models. Chen et al. (2020) concluded that the Kotiaho-Tomkins continuous model was preferred and used the model to divide the males into two allometric morphs, minors (including the previous betas and gammas) and majors (corresponding to the alphas). Both morphs have positive allometry – larger beetles have disproportionately larger weapons – but the slope is shallower in the larger (major) morph.

Packard had criticized the use of log-transformed data in Chen et al. (2020) in one of his previous commentaries (Packard, 2021). Instead, he proposed fitting a four-parameter sigmoid function through the arithmetic data and suggested that this removed the need to consider two morphs. It has, however, been demonstrated that sigmoid functions often represent bimodal, and hence dimorphic, populations (Buzatto et al., 2024).

Ultimately, this debate is of questionable interest biologically. Chen et al. (2020) noted three distinct male morphologies but modelled the allometric relationship between body size and weapon size with two lines through log-transformed data. Packard (2021) prefers a single four-parameter sigmoid curve. Both methods show that males with larger bodies have disproportionately large weapons and that the slope is shallower in the largest group of males.

Conclusions

The main objective of Chen et al. (2024) was to investigate whether metabolic costs might constrain mandible size in larger males, and we showed that indeed they might. Nothing that Packard (2025) writes casts any doubt on this, so we strongly disagree with his contention that his analysis would have led to different conclusions.

Chen et al. (2024) did not divide the males into different morphs; it is misleading for Packard (2025) to suggest otherwise. Chen et al. (2020) divided the males into different morphs, and Packard (2021) has already commented on the paper. Chen et al. (2020) found that males with larger bodies have disproportionately large weapons, but that the slope is shallower in larger males and modelled this with two lines through log-transformed data. Packard (2021) prefers a four-parameter sigmoid curve through arithmetic data, which essentially shows the same thing.

Chen et al. (2020) show a positive allometry between body and weapon size with a shallower slope in large males. Chen et al. (2024) show that this shallower slope might be the result of metabolic constraints. Nothing in Packard (2021) or Packard (2025) alters these conclusions.

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