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Life cycle and phenology of *Onthophagus vacca* (L.) in Middle Atlas (Morocco): implications for conservation and ecosystem services (Coleoptera: Scarabaeidae)

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Abstract
This work investigates the life cycle and seasonal dynamics of the dung beetle *Onthophagus vacca* in Middle Atlas ecosystems in Morocco. This species is recognized for its crucial ecological role and was studied under controlled conditions to assess its developmental stages (egg, larva, pupa, adult) and seasonal abundance in relation to environmental factors. The results show that *Onthophagus vacca* has a short life cycle with peak activity in spring, which correlates with moderate temperatures and limited rainfall. The abundance of this species is higher in sites located at higher altitudes, where climatic conditions are more favorable. This study contributes to our understanding of the ecological requirements of *Onthophagus vacca* in Morocco and highlights the importance of its conservation to preserve the ecosystem services it provides, particularly in terms of soil fertility and excreta management in agricultural environments.

Key words: *Onthophagus vacca*, seasonal dynamics, dung beetle, Scarabaeidae, reproductive cycle.

Introduction

Natural ecosystem functions are essential for sustaining the biogeochemical processes that ensure the productivity and stability of ecosystems (Cardinale et al. 2012; de Groot et al. 2002). Among these functions, dung removal and burial, key ecological processes performed by dung beetles, are essential for maintaining soil health and ensuring agricultural productivity. Dung beetles, such as *Onthophagus vacca* (L., 1767), are considered ecosystem engineers because their activities provide multiple ecological services such as reducing nuisance fly populations, improving soil structure and increasing soil fertility (Beynon et al. 2015; Hajji et al. 2024; Holter & Scholtz 2007; Kadiri et al. 2022; Losey & Vaughan 2006; Nichols et al. 2008)"DOI":"10.1111/een.12240","language":"fr","source":"resjournals.onlinelibrary.wiley.com","title":"The application of an ecosystem services framework to estimate the economic value of dung beetles to the U.K. cattle industry","URL":"https://resjournals.onlinelibrary.wiley.com/doi/10.1111/een.12240","author":[{"family":"Beynon","given":"Sarah A."},{"family":"Wainwright","given":"Warwick A."},{"family":"Christie","given":"Michael"}],"accessed":{"date-parts":[["2024",10,11]]},"issued":{"date-parts":[["2015"]]}}},{"id":1286,"uris":["http://zotero.org/users/6620718/items/BH73HWFW"],"itemData":{"id":1286,"type":"article-journal","abstract":"Dung beetles are important ecosystem engineers as they bury manure produced by animals and contribute to nutrient cycling. This study assessed the impact of four dung beetle species, a roller (Gymnopleurus sturmi. These activities thus contribute to better retention of nutrients essential for plant growth (Brown et al. 2010; Forgie et al. 2018; Johnson et al. 2016; Keller et al. 2022).

Their ecological importance has been recognized in international projects such as the "Dung Beetle Ecosystem Engineers" program in Australia, where *O. vacca* was introduced intentionally to address problems associated with the excessive accumulation of cattle dung in the south of the country (Monty 2022). This program aimed to mitigate the negative impacts of standing dung in pastures by mobilizing dung beetles to improve soil health and reduce populations of flies and other pests. The introduction of *Onthophagus vacca* into these ecosystems not only demonstrates its effectiveness in providing ecosystem services but also highlights the importance of understanding its life history to better plan long-term management strategies.

However, despite their ecological importance, dung beetles are increasingly threatened by habitat loss, intensive agricultural practices, increased pesticide and antibiotics routinely used to improve livestock health and growth (Verdú et al. 2015; Hammer et al. 2016; Martínez et al. 2017; Lumaret et al. 2022a, b)including two controls and six increasing ivermectina concentrations (3.16, 10.0, 31.6, 63.2, 100, and 316 μg IVM/kg fresh dung. These pressures compromise their ability to fulfill their ecological functions. The conservation of *Onthophagus vacca* is therefore crucial, not only to maintain these ecosystem services, but also to ensure the long-term resilience of agricultural ecosystems (Bertone et al. 2006; Hajji et al. 2024; Lastro 2006; Piccini et al. 2020; Santos-Heredia et al. 2018)Onthophagus gazella (Fabricius. Understanding its life cycle and seasonal population dynamics is crucial to identifying the key periods when this species is most vulnerable and where conservation efforts can be most effective.

The main objective of this study is to explore the life cycle and phenology of *Onthophagus vacca* under controlled conditions in Morocco, focusing not only on the developmental stages (egg, larva, pupa, adult), but also on the seasonal variations in its abundance and activity. Although the impact of this species on soil fertilization and plant growth has already been documented in a previous work (Hajji et al. 2024), this study proposes a novel analysis of the complete life cycle of *O. vacca*, providing essential data for understanding its population dynamics and justifying its conservation.

Material and methods

Study sites and beetle's collection

Four sites were selected in Morocco for this study to monitor fluctuations in the abundance of *O. vacca* in its natural habitat. The sites were located between the Sais plain and the Middle Atlas: Fès-Sais (site A: 33°54' N – 4°59' W; elevation 609 m); Immouzzer (site B: 33°47′ N - 4°59′ W; elevation 898 m), and two sites close to the town of Ifrane (site C: Ifrane I, 33°32′ N - 5°09′ W; elevation 1631 m; and site D: Ifrane II, 33°33′ N - 5°10′ W; elevation 1613 m) . These sites differ in several mesological factors (bioclimatic zones, elevation, soil and vegetation cover) (Hajji et al. 2023 and Hajji et al. 2025).

To study the phenology of *Onthophagus vacca*, three baited traps of the CSR type (Lobo et al. 1988) were set simultaneously at each site and collected weekly for one year between 2018 and 2019. These traps were baited with fresh cattle dung, and captured specimens were transported to the laboratory for identification (Hajji et al. 2023).

Specimens for laboratory breeding were collected manually at site C (Ifrane II). Manual collection involved

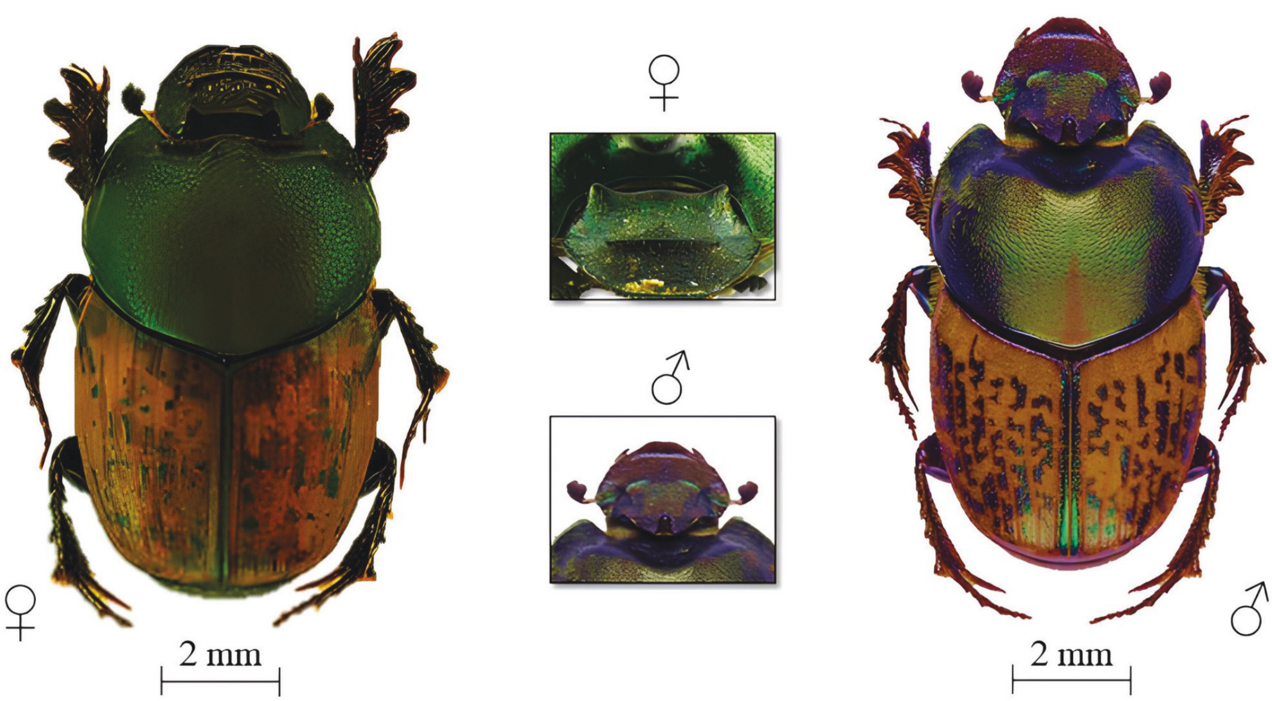

Fig. 1 – Sexual dimorphism in *Onthophagus vacca*: morphological differences between the sexes (♀ and ♂).

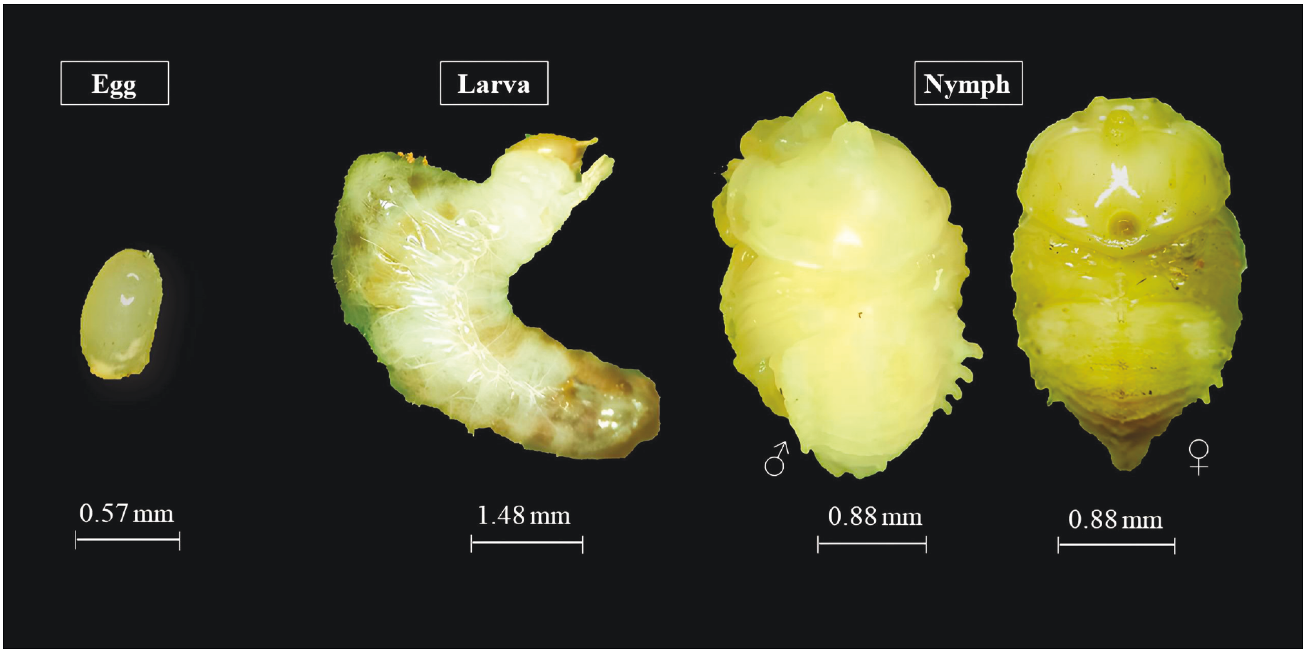

Fig. 2 – Development of *Onthophagus vacca* (mature egg, 3rd instar larva, pupa) and sexual dimorphism in the pupal stage.

inspecting semi-fresh sheep droppings and recovering specimens by digging the soil to a depth of 3-10 cm beneath the droppings.

Identification and sexual separation

Captured specimens were transported in aerated containers containing soil and dung. On arrival at the Laboratory of Biotechnology, Conservation and Valorisation of Natural Resources, Faculty of Sciences Dhar El Mehraz, the specimens were identified using a binocular magnifying glass to confirm their identification. Sexual dimorphism has made it possible to separate the males, recognizable by an almost non-existent frontal carina and a high, rectangular blade-shaped vertex carina, which lies backwards and ends in a small upright median horn, from the females, recognizable by a pronounced frontal carina and a high vertex carina, which is generally toothed at the ends (Fig. 1).

Laboratory rearing conditions

The beetles were reared in the laboratory in circular plastic boxes, 10 cm in diameter and 25 cm deep, filled with sieved soil from the capture site (silty clay soil). The boxes were perforated to ensure adequate aeration and each box contained 5 pairs (male and female). The temperature was maintained at 27°C with a relative humidity of 60-70%, and a photoperiod of 12 hours of light was applied to simulate natural conditions. The beetles were fed with fresh cattle dung, which was changed every three days.

Life cycle monitoring

The life cycle of the beetles was monitored once the pairs had produced their brood masses. Each brood mass containing an egg was removed and placed in individual terrariums with moist soil. Monitoring was carried out three times a week, with measurements taken at each stage of the life cycle: egg, larva, pupa and adult. The size and weight of eggs, larvae (3rd instar) and pupae were recorded, as well as the size and weight of emerged adults (Fig. 2).

Environmental data

Monthly meteorological data (maximum, minimum and mean temperature, mean precipitation, relative humidity and wind speed), were provided by the Sebou River Basin Agency) (www.abhsebou.ma). Meteorological data from the Ifrane weather station were used to characterize both sites C and D due to their proximity. The altitude and geographical coordinates of the sites were determined using a GPS device (Garmin eTrex 10).

Statistical analysis

The Kruskal-Wallis test, followed by a Wilcoxon test, was used to compare species abundance between the four sites and the different months of the year. ANOVA was not used because the conditions of normality and/or homoscedasticity were not fulfilled.

Results

Life cycle of *Onthophagus vacca*

The laboratory study showed that the complete life cycle of *Onthophagus vacca* lasted 39.0 ± 1.18 days (N = 10) (Fig. 3). The embryonic stage lasted 3.0 ± 0.3 days (N = 10). The larvae pass through three distinct stages over the next 22.0

± 0.89 days (N = 10), with significant growth at each stage. The third instar larvae reached an average length of 16 ± 0.53 mm and was characterized by a curved 'C' shape, a dorsal hump, a segmented body and a brown head. The pupal stage lasted 14.0 ± 0.8 days (N = 10). During this stage, nymphs averaged 7.0 ± 0.59 mm in length and 5.05 ± 0.65 mm in width, with secondary sexual characteristics allowing easy identification of males and females. At emergence, the adult body size was 7.28 ± 0.63 mm in length.

Seasonal abundance and population dynamics

The abundance of *O. vacca* was significantly higher at sites C and D compared to sites A and B (Fig. 4, left). The highest observed abundance at all sites was recorded during month 4 (April) (Fig. 4, right) and this result was statistically significant ($p \leq 0.05$). This peak continued (but to a lesser extent) in month 5, followed by a fall in month 6 (June) and then a recovery in July (Fig. 5). The main peak (April) coincided with heavier rainfall than in previous months, combined with moderate temperatures (Fig. 5).

These results show that the optimum temperature for emergence of this species ranged between 5°C and 18°C (Fig. 5). This spring species tolerates average temperatures up to 30°C, but becomes inactive when temperatures exceed this threshold, as in months 6 and 8.

Discussion

Under laboratory conditions, the development of *O. vacca* from egg to adult emergence takes approximately 39 days, a relatively intermediate time compared to that

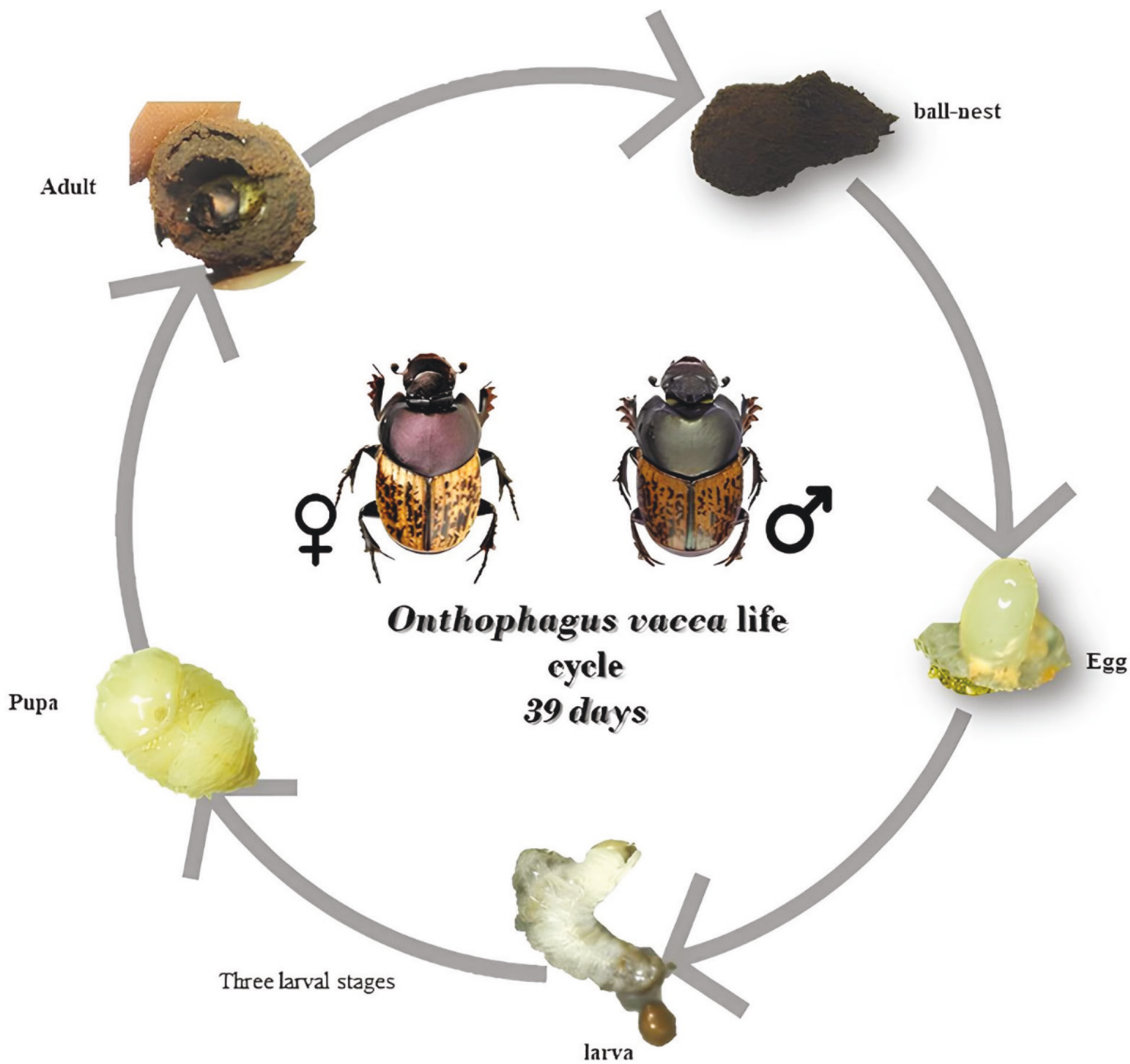

Fig. 3 – *Onthophagus vacca* life cycle.

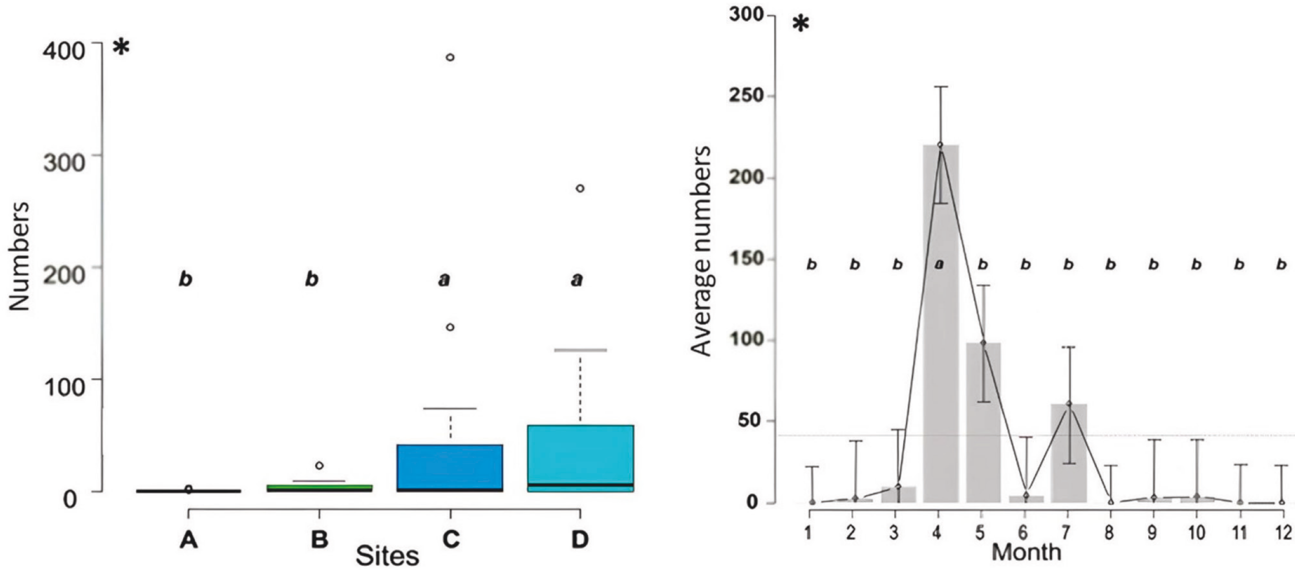

Fig. 4 – The overall difference in numbers between sites and months after the non-parametric Kruskal-Wallis test. Means with the same letters are not significantly different. Error bars represent the standard deviation (sd) of observations. p-values: * $p \leq 0.05$.

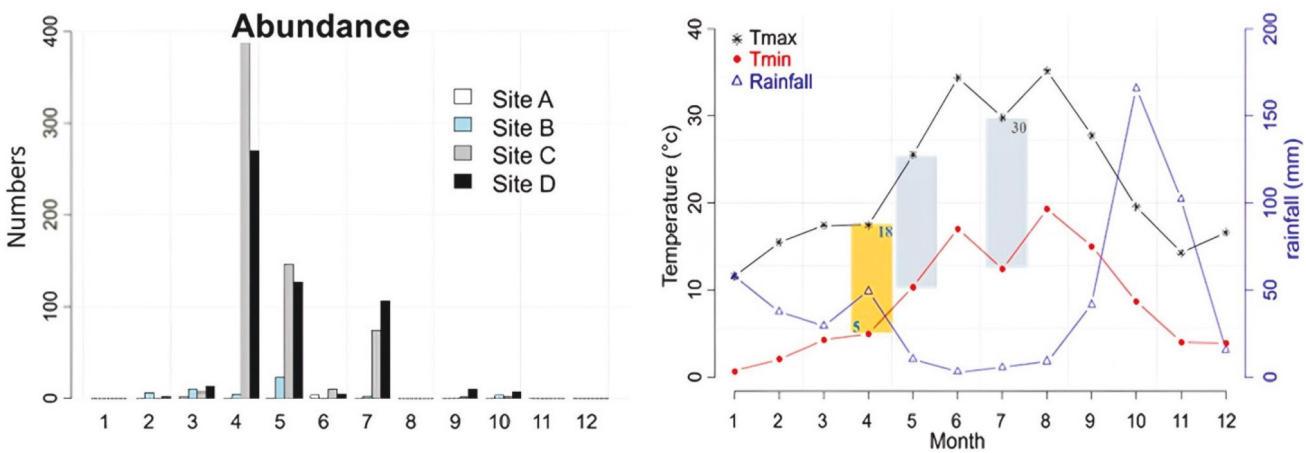

Fig. 5 – *Onthophagus vacca* abundance at the four collection sites over the 12-month sampling period (left). Meteorological data (temperature and precipitation) for sites C and D (Ifrane I and II) over the same 12-month sampling period (right).

known for other species: 21 days for *Onthophagus oklahomensis* Brown (Howden & Cartwright 1963), but up to 46 days for *O. depressus* Harold (Hunter et al. 1996) and up to 51-70 days for *O. stylocerus* Graëlls (Romero-Samper & Martín-Piera 1995). Arellano et al. (2017), Prameela & Sabu (2020) and Martinez et al. (2022) also reported other developmental values for different *Onthophagus* species, but always within the same order of magnitude.

The rearing conditions for *O. vacca* were maintained at a temperature of 27°C and a relative humidity of 60-70%, i.e. within a high range of the optimal conditions for activity of the species in the field (Fig. 5), insofar as temperature and soil humidity can play a role in modulating the life cycles. This was highlighted by Arellano (1992) who showed that the emergence peaks of *O. incensus* Say varied in different locations of the same region (central Veracruz, Mexico). In Morocco, *Onthophagus vacca* is essentially a spring species, active at a time of year with moderate temperatures and relatively low rainfall, but where soil moisture, which is still high at this time of year, plays a crucial role in the size of the individuals of the new generation that emerge, regardless of the amount of food available to the parents (Sowig 1996). This observation is consistent with studies by Birkett et al. (2018) and Gaston & Chown (1999)even if the pattern of tolerance of species assumed by the climatic variability hypothesis is correct, an increase in altitudinal range with increasing elevation need

not necessarily follow. However, although sampling has been limited, there does appear to be an elevational increase in altitudinal range for this species assemblage.","container-title":"Oikos","DOI":"10.2307/3546663","ISSN":"0030-1299","issue":"3","note":"publisher: [Nordic Society Oikos, Wiley]","page":"584-590","source":"JSTOR","title":"Elevation and Climatic Tolerance: A Test Using Dung Beetles","title-short":"Elevation and Climatic Tolerance","volume":"86","author":[{"family":"Gaston","given":"Kevin J."},{"family":"Chown","given":"Steven L."}],"issued":{"date-parts":[["1999"]]}}}],"schema":"https://github.com/citation-style-language/schema/raw/master/csl-citation.json"}
, who noted that dung beetles are often thermophilic and prefer moderate temperatures for activity and reproduction. However, some species show increased activity during periods of heavy rainfall, while others prefer summer temperatures, demonstrating a diversity of seasonal adaptations within the Scarabaeidae family (Calatayud et al. 2021; Nyamukondiwa et al. 2018)feeding and development. This seasonal flexibility allows different species to temporally and ecologically disperse according to climatic conditions, thereby minimizing interspecific competition. The life history traits observed in *O. vacca*, such as rapid maturation from egg to teneral adult, show strong ecological adaptability, like that of *O. cervus* in India, with high fecundity and a moderately short life cycle (Prameela & Sabu 2020). These characteristics allow *O. vacca* to maintain stable populations despite environmental fluctuations, making this species a resilient component of Moroccan agricultural landscapes. This resilience is essential to ensure its role in the ecosystem, particularly in nutrient recycling (Hajji et al. 2024). *Onthophagus vacca* is widespread in the western Palearctic, especially in southern and south-central Europe, and extends its range towards northern Africa (Morocco and Algeria). In central Europe, *O. vacca* appears to be absent north of 50° latitude and is completely absent in the Alps, whereas it is found in the higher mountains of southern Europe (Rössner et al. 2010). This wide range means that this rather thermophilic species is exposed to somewhat contrasting climatic conditions, with the Moroccan populations studied being mainly at high altitude (Ifrane). *Onthophagus vacca* seems to overwinter as adults and appears quite early in the year, with a peak of activity in April-May, with a second peak in July (Fig. 4). In the context of climate change, understanding the life cycle and phenological behavior of *O. vacca* is crucial for predicting its response to future conditions. Studies by Sheldon & Tewksbury (2014)biogeography, and life history, with large consequences for ecology, evolution, and the impacts of climate change. Based on the seasonality hypothesis, greater annual temperature variation at high latitudes should result in greater thermal tolerance and, consequently, larger elevational ranges in temperate compared to tropical species. Despite the mechanistic nature of this hypothesis, most research has used latitude as a proxy for seasonality, failing to directly examine the impact of temperature variation on physiology and range size. We used phylogenetically matched beetles from locations spanning 60° of latitude to explore links between seasonality, physiology and elevational range. Thermal tolerance increased with seasonality across all beetle groups, but realized seasonality (temperature variation restricted to the months species are active show that dung beetles may experience selective pressures due to thermal changes, which could affect their breeding periods and ability to survive in warmer environments.

Conclusions

This study contributes to our understanding of the biology and ecology of *O. vacca*, shedding light on its life cycle and environmental preferences in the Middle Atlas. Comparison with previous studies highlights the ability of this species to adapt to specific climatic conditions and to play an essential role in maintaining ecosystem services. The conservation of *O. vacca* should be considered a priority in agricultural ecosystems due to its contribution to soil fertility and manure management (Hajji et al. 2024). Future research will focus on the interaction of *O. vacca* with other dung beetle species and their direct effects on soil properties. This could help to develop sustainable management strategies and ensure the resilience of these ecosystems in the face of increasing anthropogenic pressures.

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