

Revisión

Review of ecophysiological research in dung beetles (Coleoptera: Scarabaeoidea): actual state and future studies for Argentina

Revisión de investigaciones ecofisiológicas en escarabajos estercoleros (Coleoptera: Scarabaeoidea): estado actual y estudios futuros para Argentina

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Abstract: Insects, particularly dung beetles, are highly sensitive to environmental changes due to their dependence on climatic variables like temperature and humidity. These variables control numerous physiological and biochemical functions, making the study of insect ecophysiology crucial for understanding their spatial and temporal distribution. Dung beetles play vital roles in ecosystems, such as nutrient recycling, soil aeration, greenhouse gas mitigation, seed dispersal, and improving livestock health. Due to their sensitivity to environmental changes and antiparasitic drugs excreted in cattle feces, they serve as excellent bioindicators. Extensive studies worldwide have examined the ecophysiological responses of dung beetles to temperature, humidity, residues of veterinary medications excreted in cattle dung, and trophic preferences, revealing significant impacts on their survival and ecosystem functions. In Argentina, although some local and regional studies have explored some of these aspects, comprehensive ecophysiological research remains limited. Future studies in Argentina should focus on the effects of temperature, humidity, antiparasitic drugs, and trophic resources, to enhance the understanding of dung beetles' ecophysiological responses. Such research is essential for developing effective conservation strategies, particularly in regions with high cattle production and diverse dung beetle populations, ensuring the maintenance of their important ecological functions.

Keywords: Antiparasitics, Ecophysiology, Humidity, Insects, Temperature.

Resumen: Los insectos, en particular los escarabajos estercoleros, son muy sensibles a los cambios ambientales debido a su dependencia a variables climáticas como la temperatura y la humedad. Estas variables controlan numerosas funciones fisiológicas y bioquímicas, haciendo que el estudio de la ecofisiología de los insectos sea crucial para comprender su distribución espacial y temporal. Los escarabajos estercoleros desempeñan funciones vitales en los ecosistemas, como el reciclaje de nutrientes, aireación del suelo, mitigación de los gases de efecto invernadero, dispersión de semillas y mejora de la salud del ganado. Debido a su sensibilidad a los cambios ambientales y drogas antiparasitarias excretadas en las heces del ganado, sirven como excelentes bioindicadores. Extensos estudios en todo el mundo han examinado las respuestas ecofisiológicas de los escarabajos estercoleros a la temperatura, a la humedad, a residuos de productos médico-veterinarios eliminados

en los excrementos del ganado, y a preferencias tróficas, revelando impactos significativos sobre su supervivencia y las funciones del ecosistema. En Argentina, aunque algunos estudios locales y regionales han explorado algunos de estos aspectos, la investigación ecofisiológica exhaustiva sigue siendo limitada. Futuros estudios en Argentina deberían centrarse en los efectos de la temperatura, la humedad, las drogas antiparasitarias, y los recursos tróficos para mejorar la comprensión de las respuestas ecofisiológicas de los escarabajos estercoleros. Este tipo de investigación es esencial para desarrollar estrategias de conservación eficaces, especialmente en regiones con una elevada producción ganadera y diversas poblaciones de escarabajos estercoleros, garantizando el mantenimiento de sus importantes funciones ecológicas.

Palabras clave: Antiparasitarios, Ecofisiología, Humedad, Insectos, Temperatura.

IMPORTANCE OF STUDIES IN INSECT PHYSIOLOGY

Insects are among the most sensitive organisms to environmental changes because they depend on environmental and ecological variables (*e.g.*, temperature, humidity, solar radiation, infrared radiation, wind, trophic resources, pharmaceutical antiparasitics) from the molecular to the macroecological level (Lee & Denlinger, 1991; Chown & Nicholson, 2004; Dixon et al., 2009; Kingsolver, 2009; Verdú et al., 2010, 2013; Reis et al., 2011; Andersen et al., 2015). Among the environmental variables that most affect insects are temperature and humidity; both control several biochemical and physiological functions, behavior, and development in insects (Kingsolver, 2009; Reis et al., 2011). In terrestrial ecosystems, insects face a wide variety of climatic conditions among different habitats and throughout the day and year (Chown et al., 1995), and their ecophysiological response determine their spatial and temporal distribution (Bartholomew & Heinrich, 1978; Verdú et al., 2004, 2007). Previous studies have examined the morphological, ethological, and ecophysiological responses of insects to environmental changes at local, regional and global scales, and it was observed that the ecophysiological response is the one that explains the patterns observed in nature (Tauber & Tauber 1986; Chown et al., 2002; Moriyama & Numata, 2019; Nervo et al., 2021a; Giménez Gómez et al., 2022, 2025; Lehmann & Wheat, 2022; Gonzalez et al., 2023).

Given the sensitivity of insects to environmental changes, the study of their ecophysiological responses is highly relevant in the short term due to human-induced environmental disturbances (*e.g.*, replacement of natural environments with disturbed ones, livestock) and in the long term due to climate change (global warming) (Dirzo & Raven, 2003; Nunez et al., 2019; Verdú et al., 2018, 2019). All insect species have thermal and metabolic limits that determine their tolerance to environmental changes; outside these limits, they lose their motor skills and become vulnerable to predation or exposure to lethal environmental conditions (such as extreme temperature and humidity) (Byrne et al., 2004). These limits, together with the capacity to regulate changes in ecophysiological variables (*e.g.*, thermoregulation), determine the thermal niche of each species (Verdú & Lobo, 2008). This axis of the ecological niche is used to explain not only the current distribution and response of insect species but also their future distribution and response to environmental changes (mechanistic distribution models) (Kearney & Porter, 2004, 2009; Peterson et al., 2015). Understanding the thermal niche and the response of insect species to short- and long-

term environmental changes is crucial for developing conservation strategies to prevent future species loss, especially for those important to the ecosystem, such as dung beetles (Nichols et al., 2007, 2008; Giménez Gómez et al., 2020a, 2022). This is critical in these times when many ecosystems are losing the right conditions for species survival (Nunez et al., 2019).

IMPORTANCE OF DUNG BEETLES

Dung beetles are one of the most studied insect groups in ecology because they exhibit high species richness and abundance (Ocampo & Hawks, 2006; Spector, 2006), and they are sensitive to anthropogenic disturbances (Verdú et al., 2007; Gardner et al., 2008; Tonelli et al., 2017), either by human-induced changes in the trophic resource diversity (Culot et al., 2013) or climatic conditions (Osberg et al., 1993; Oliveira-Filho & Fontes, 2000; Broennimann et al., 2012). Additionally, their taxonomy is relatively stable and well-known (Philips et al., 2004), and they play a crucial role in ecosystem functioning (Hanski & Cambefort, 1991; Andresen & Feer, 2005; Nichols et al., 2008; Verdú et al., 2018). Through their ecological functions, the dung beetles contribute significantly to soil health, climate regulation, and livestock areas.

They recycle nutrients by breaking down animal feces, which enriches the soil with organic matter. This process enhances soil fertility, improves water retention, and reduces soil erosion. By burying dung, dung beetles aerate the soil and increase its organic content, benefiting plant growth and reducing the prevalence of pest insects like flies (Nichols et al., 2008). They help to mitigate greenhouse gas emissions by breaking down dung, which reduces methane and carbon dioxide released from livestock dung. This activity is particularly important in livestock areas where large quantities of animal dung are produced (Slade et al., 2016; Verdú et al., 2019). They also play a role in seed dispersal, as some plant seeds are transported and buried by dung beetles, enhancing plant propagation and maintaining healthy ecosystems (Shepherd & Chapman, 1998; Nichols et al., 2008). In livestock areas, dung beetles improve pasture quality by distributing nutrients and reducing parasite loads in livestock by burying dung, which interrupts the life cycles of many parasitic species. This activity helps maintain healthier livestock and reduces the need for chemical treatments (Nichols et al., 2008). Overall, dung beetles are indispensable for maintaining ecological balance and supporting sustainable livestock practices. Their contributions highlight the importance of conserving these beneficial insects to ensure the health and productivity of ecosystems globally.

ECOPHYSIOLOGICAL STUDIES CONDUCTED THROUGHOUT THE WORLD

Due to the great sensitivity of dung beetles to changes in environmental conditions, to ecological condition (*e.g.*, trophic resources), and their important ecosystem functions, the study of their physiology and their ecophysiological response to environmental variables associated with human activity (*e.g.*, environment replacement, antiparasitic drugs, antibiotics, herbicides) have been widely conducted worldwide. In general, important ecophysiological studies have been carried out on dung beetles associated with temperature, humidity, antiparasitic drugs excreted in cattle feces, antibiotics, herbicides, and trophic resources. In this work, a total of 64 scientific articles associated with dung beetle's physiology were reviewed, six of which were conducted in Argentina (Table I). Table I includes both studies performed outside Argentina and in the country. The search for articles was conducted using Google Scholar with the keywords 'dung beetles physiology', 'antiparasitics and dung beetles physiology', 'herbicides and dung beetles physiology', 'antibiotics and dung beetles physiology', 'trophic resources and dung beetles physiology' and through consultations with specialists.

In summary, from all these studies, it can be highlighted that not only do changes in temperature and humidity have negative effects on the ecophysiology (harmful impacts on both the physiology and ecological roles) of dung beetles, but so do the antiparasitic drugs administered to cattle, and herbicides and antibiotics to a lesser degree. Changes in physiology associated with the type of resources used for feeding have also been observed. This demonstrates the great sensitivity of this group of insects to environmental changes, to ecological variables, and the drugs used for parasite control in cattle. This sensitivity makes dung beetles excellent indicators of environmental changes. Regarding the use of ecotoxic synthetic pharmaceutical anthelmintics (*e.g.*, ivermectin), it is important to note that alternatives are being found that are not lethal to dung beetles, such as phytochemical anthelmintics (*e.g.*, thymol, carvacrol, cinnamaldehyde) (Verdú et al., 2023). The latter has been proposed in Spain but given the significant negative impact that previous studies have demonstrated the pharmaceutical antiparasitics present, it is crucial to conduct these studies in other countries to begin the process of replacing the lethal antiparasitics and thus avoid future loss of dung beetle species and their ecosystem functions.

ECOLOGICAL STUDIES CARRIED OUT IN ARGENTINA

In Argentina, the response of dung beetles to environmental disturbances has been studied at both local and regional scales at the community level (Gómez-Cifuentes et al., 2017, 2018, 2023; Giménez Gómez et al., 2018a, 2022, 2025; Guerra Alonso et al., 2019, 2020, 2021, 2022, 2023; Guerrero et al., 2024). At the local scale, research indicates that dung beetles are highly sensitive to environmental changes, with greater disturbances leading to lower diversity and abundance (Gómez-Cifuentes et al., 2017, 2018; Giménez Gómez et al., 2018a, 2022; Guerra Alonso et al., 2019, 2021; Guerrero et al., 2024). At the regional scale, dung beetle communities exhibit varying responses depending on the environmental conditions of each region (Giménez Gómez et al., 2025; Guerra Alonso et al., 2020, 2022, 2023). To explain these ecological patterns, researchers have assessed multiple ecological traits, including food preference, morphological, behavioral and physiological characteristics (Wurmitzer et al., 2017; Giménez Gómez et al., 2018b, 2020a, 2020b, 2022, 2025; Bobadilla et al., 2024). It is important to note that research has been conducted on the ecosystem functions of dung beetles and how these functions are affected by environmental disturbances (Maldonado et al., 2019, 2023; Gómez-Cifuentes et al., 2023; Vespa et al., 2024); as well as studies on the association of mouthparts with respect to trophic preferences and studies on standardization of functional traits (Giménez Gómez & Tonelli, 2022; Giménez Gómez et al., 2023).

Among the studies conducted in Argentina, five have focused on ecophysiological research to explain the patterns observed in nature (Giménez Gómez et al., 2017, 2020a, 2022, 2025; Verdú et al., 2019, 2022). Local-scale studies have found that ecophysiology, rather than morphology and ethology, explains temporal (Giménez Gómez et al., 2017, 2022; Verdú et al., 2022) and spatial distribution (Giménez Gómez et al., 2020a, 2022; Verdú et al., 2019, 2022) of dung beetles. In these studies, variables associated with temperature (variables associated with thermal stress and thermal limits) and metabolic rate (variations in the CO₂ emissions by respiration) have been used to investigate the response of species to heat stress. By subjecting them to extreme temperatures, we have been able to determine which species are most tolerant or most susceptible to environmental changes both locally and regionally (Giménez Gómez et al., 2022, 2025). This knowledge has allowed us to suggest strategies for the conservation of some dung beetle species. We have also used variables associated with flight, endothermy, and thermoregulation, which on the one hand helped us to explain the fact that some species are able to tolerate short-term environmental changes, and which also helped us to suggest what will happen in the long term with some dung beetle species.

Currently, in Argentina, studies are being conducted on larger scales using mechanistic distribution models that incorporate basic

ecophysiology to explain the current potential distribution of some species and their potential future distribution based on their thermal limits. This approach will allow researchers to predict how species will respond to rising temperatures in the coming years, providing information on future distribution patterns based on their physiological characteristics (Kearney & Porter, 2004, 2009; Evans et al., 2015; Phill & Thomson, 2015; Maino et al., 2016). Argentina will be a pioneer in applying these models to dung beetles, and it is expected that the use of these models will be highly beneficial when replicated in other countries. This will contribute significantly to the ecophysiological studies of dung beetles and their conservation.

Research topic	Ecophysiological response	Reference
Response to temperature: thermoregulation in flight and thermal stress	Body temperatures: thoracic temperatures (Tth).	Ybarrondo & Heinrich, 1996; Mena, 2001
	Body temperatures: Tth and abdominal temperature (Tab).	Verdú et al., 2004, 2012
	Body temperature (Tb); body mass (WT).	Verdú et al., 2006
	Body temperatures: Tth and Tab; abdominal temperature excess ratio (Rab); endothermic capacity: temperature excess (Tex) measured as the difference between Tb and ambient temperature (Tenv); WT; supercooling point of the haemolymph.	Verdú & Lobo, 2008
	Start stress temperature (SST); critical thermal maximum (CTmax); upper lethal temperature (ULT). Ranges of: heating rate on supra-optimal activity (SAR); heating rate on heat stress (HSR); heating rate on heat coma (HCR).	Gallego et al., 2018
Thermoregulation patterns, endothermia in flight and associated to other activities	Body temperatures: Tb and temperature of the metathorax; WT.	Bartholomew & Heinrich, 1978
	Body temperatures: Tth.	Heinrich & Bartholomew, 1979
	Body temperatures: Tb and Tex.	Verdú et al., 2007
	Heat response: heat stress (SHST); heat regulation temperature HRT; CTmax; ULT. Cold response: Start of cold stress temperature (SCST); Start of cold stupor temperature (CST). CO ₂ and H ₂ O emissions.	Verdú et al., 2019
	Heat response: SST; HRT; CTmax; ULT. CO ₂ and H ₂ O emissions.	Verdú et al., 2022
Thermal tolerance to cold and/or heat (thermal limits)	Body temperatures: Tth and Tab; Tex.	Chown et al., 1995
	Super cooling point (SCP); WT.	Verdú, 2011
	Start of activity: heating rate (HR); chill coma recovery range (CCRR); chill coma recovery time (CCRT). Cold response: SCP; chill coma temperature (CCT); cooling rate (CR); chill coma range (CCR). SAR; SST; HSR; heat regulation temperature (HRT); thermoregulation range (TR); HCR; ULT; CTmax.	Gallego et al., 2016
	Cold response: CCRT; HR; CCT; CR. Heat response: SST; SR; HRT; HCR; TR; ULT; CTmax.	Gallego et al., 2017
	Cold response: SCP; CR; HR; CCRT; Critical thermal minimum (CTmin)	Gallego et al., 2024
	WT; Optimal temperature; Primary and secondary peak of activity; Tolerance period.	Giménez-Gómez et al., 2017
	CTmin, CTmax, heat stupor, cold coma.	Gaston & Chown, 1999; Birkett et al., 2017
	CTmax and activity time.	Gotcha et al., 2021a
	CTmin and CCRT.	Gotcha et al., 2021b
	CTmax and heat knockdown time (HKDT). Acclimation temperatures of variable high (VT-H) and acclimation temperatures of variable low (VT-L).	Machekano et al., 2021
Respiratory metabolism and changes in metabolic rate	Body temperatures: Tth and Tab; Tex.	Chown et al., 1995
	Responses to constant, low fluctuation, or high fluctuation temperature treatments.	Sheldon et al., 2020
Respirometry (respiration and respiratory regulation)	O ₂ emission	Holter & Spangenberg, 1997
	Discontinuous gas exchange cycles (DGC); CO ₂ and O ₂ emissions.	Davis et al., 1999; Duncan & Byrne, 2000, 2002; Byrne & Duncan, 2003
	DGC; CO ₂ and H ₂ O emissions.	Duncan, 2002
	DGC; CO ₂ emission.	Duncan & Byrne, 2005
	Respiratory gas exchange: CO ₂ emission cycles; Pressure within the tracheal system (P _{TS}) and the subelytral cavity (P _{SEC}).	Duncan et al., 2010
Temperature in synergy with antiparasitic drugs	Reproduction, development, survival	Esquivel-Román et al., 2024
Heating process of internal body parts	Thorax length (l), width (w) and height (h); Pseudo-volume (V); Body dry mass; weight of chitin per volume unit (ChW).	Amore et al., 2017
Thermal and metabolic passivity at different stages of development	Thermal fluctuations; CO ₂ emission	Carter & Sheldon, 2020; Fleming et al., 2021
Reproductive behaviors in response to temperature	Oviposition rate. Brood ball (BB) number; Development threshold; Oviposition cycles	Tyndale-Biscoe, 1978; Tyndale-Biscoe et al., 1981
	BB number and BB size; Burial depth.	Kirkpatrick & Sheldon, 2022
Effects of antiparasitic drugs	Olfactory detection by olfactometer test; Olfactory response by electroantennography (EAG); Spontaneous isometric force	Verdú et al., 2015
	Clutch size; Sex and male morph ratio; Body condition: body length, body dry mass, wing fluctuating asymmetry, lipid and muscle content	González-Tokman et al., 2017
	Offspring number; Sex ratio; Body condition: body size and male horn length	Baena-Díaz et al., 2018
	Olfactory response by EAG. Biomagnification and body distribution	Verdú et al., 2018
	Biomagnification and body distribution	Verdú et al., 2020
	Body condition: Body size, lipid mass, and muscle mass	Souza et al., 2018; Villada-Bedoya et al., 2019
	Post-mortem and in vivo tissues	Ortiz et al., 2017
	CO ₂ emission; Heat shock protein 70 (Hsp70); Total proteins; Total antioxidant capacity (TAC); Oxidative damage to lipids (TBARS - lipid peroxidation).	Villada-Bedoya et al., 2021
	Body condition: Body size, muscle mass and body fat mass	Alcántara et al., 2023
	BB number; Offspring number; Sex ratio; Survival of adults; Fitness index; Fecundity; Reproduction	Cruz Rosales et al., 2012; Martínez et al., 2017; Huss et al., 2021; Esquivel-Román et al., 2024
		González-Tokman et al., 2024
		González-Tokman et al., 2024

Table I.

Ecophysiological studies on dung beetles to environmental conditions (temperature and humidity), antiparasitic drugs, herbicides, antibiotics, and trophic resources.

Studies carried out in Argentina are highlighted in bold type.

FUTURE ECOPHYSIOLOGICAL STUDIES FOR ARGENTINA

Considering all the studies carried out abroad and in Argentina, it can be said that many ecophysiological studies have yet to be conducted in Argentina. Regarding *temperature*, we need to deepen the study of its effect on thermal stress and metabolic rate, the lower thermal limits and thermal stress associated with cold. Additionally, we need to explore more variables associated with both heat and cold, the effect of temperature on the cuticle and exoskeleton, the effect of solar and infrared radiation on body temperature, the impact of temperature on body lipids and fat in general, and the effect of temperature on oviposition and developmental stages in dung beetles. Expanding our understanding of species' responses to temperature changes in Argentina will enable a more precise assessment of their susceptibility to environmental shifts. This knowledge will be essential for developing effective conservation strategies to prevent future species loss due to global warming.

Considering the studies on the effects of changes in humidity - temperature, or only humidity, and the application of herbicides, antiparasitic drugs and antibiotics on cattle, and their impact on the ecophysiology of dung beetles, it should be noted that none of these studies have been conducted in Argentina. Research in the country has only examined water loss and water volume variations under heat stress (Verdú et al., 2019, 2022; Giménez Gómez et al., 2022, 2025). These studies would greatly contribute to the understanding of the ecophysiological response of these insects to environmental changes and the use of antiparasitic drugs, while also promoting the exploration of less toxic alternatives in livestock management to prevent species loss.

Regarding *antiparasitic drugs*, in Argentina, only studies on the impact of these drugs (ivermectin, moxidectin, doramectin, eprinomectin, among others) on the diversity and abundance of insects or arthropods in general that inhabit cattle feces have been carried out (Suárez et al., 2003, 2009; Iglesias et al., 2006, 2011), but no study has focused only on dung beetles. Considering that Argentina has historically been one of the countries with the highest beef production and per capita beef consumption per year (Arrieta et al., 2020; Bifaretti et al., 2023) and that the diversity and abundance of dung beetles are high in some regions of the country (Giménez Gómez et al., 2018a; Gómez-Cifuentes et al., 2018, 2023; Guerra

Alonso et al., 2020, 2022), it is of extreme relevance to evaluate the impact of antiparasitic drugs not only on the diversity and abundance of the species but also on their ecophysiological responses.

Finally, it is crucial to highlight that further research on dung beetle ecophysiology would not only enhance our understanding of how these species respond to environmental changes in Argentina but also contribute to global scientific knowledge. Given the current global threats to dung beetle diversity—such as excessive use of antiparasitic drugs, habitat loss due to environmental disturbances, and global warming—it is essential to advance physiological research. Improving our understanding in this area will be key to preventing future loss of dung beetle species and safeguarding the vital ecosystem functions they perform.

DATA STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

COMPETING INTERESTS

The authors have declared that no competing interests exist.

AUTHORS CONTRIBUTIONS

VCGG, JRV; Bibliography search: VCGG, JRV, VC; Writing - original draft preparation: VCGG; Revision of final draft and approval for publication: VCGG, JRV, VC.

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