Daily dynamics of herbivores and natural enemies on an extrafloral nectary-bearing plant in a Neotropical wetland

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Abstract

Interactions among plants, herbivores, and natural enemies are central to community ecology, yet most studies focus only on diurnal patterns, overlooking temporal variation across the day-night cycle. Here, we describe the composition and temporal dynamics of arthropod assemblages associated with *Ipomoea carnea* (Convolvulaceae), a widespread macrophyte with extrafloral nectaries in the Brazilian Pantanal. Over one year, we surveyed 30 plants monthly in three daily periods (morning, afternoon, night), documenting herbivores (specialists and generalists) and natural enemies (ants, wasps, and spiders). We recorded 1,996 herbivores and over 19,000 natural enemies, revealing clear temporal partitioning: ants were more abundant during the day and coincided with lower herbivore abundance, while spiders peaked at night and were associated with reduced occurrence of specialist herbivores. Wasps were less abundant overall but showed activity concentrated during daytime. These patterns suggest complementary roles of natural enemies across the daily cycle, resulting in continuous pressure on herbivores. Our findings highlight *I. carnea* as a natural platform to study arthropod community dynamics and provide a critical baseline for both ecological theory and conservation efforts in one of the world’s most threatened wetlands.

Introduction

Ecological interactions are highly variable because organisms are interconnected across multiple trophic levels (Del-Claro 2012). Among these, ant–plant mutualisms mediated by extrafloral nectaries (EFNs) are some of the most studied examples (Heil & McKey 2003; Rosumek et al. 2009; Rico-Gray & Oliveira 2007), yet antagonistic interactions such as herbivory and predation are equally central in regulating populations within ecosystems (Maron et al. 2002; Snyder et al. 2006). Together, these processes’ structure complex systems involving plants, herbivores, and natural enemies (Oliveira & Del-Claro 2005; Robinson et al. 2017).

Extrafloral nectaries are widespread traits that attract ants, wasps, and spiders, providing indirect protection against herbivores while shaping arthropod community composition (Heil & McKey 2003; Lange et al. 2021; Alencar et al. 2023; Souza et al. 2024). Despite extensive research on EFN-mediated interactions, most studies have been restricted to daytime observations, overlooking potential diel variation in the activity of natural enemies and herbivores (Yamawo et al. 2014). Recent evidence suggests that temporal turnover in arthropod assemblages is an underexplored but fundamental aspect of community ecology, as natural enemies often display contrasting diel activity that may result in complementary effects on herbivore suppression (Oliveira & Del-Claro 2005; Snyder et al. 2006).

Documenting such temporal dynamics is particularly relevant in wetlands, where environmental heterogeneity and seasonal hydrology strongly influence community assembly (Junk et al. 2006; Meurer et al. 2015; Nunes da Cunha et al. 2023). The Pantanal, the largest Neotropical wetland, harbors exceptional biodiversity (Pott et al. 2011a, b; Dambros et al. 2018; Bulbol et al. 2023) but faces increasing threats from fire, droughts, and hydrological alteration (Tomas et al. 2019; Leal Filho et al.

2021; Marengo et al. 2021). In this context, EFN-bearing plants represent natural platforms to examine how daily cycles of activity mediate species interactions and how such interactions may be disrupted in threatened ecosystems.

Ipomoea carnea (Convolvulaceae) is a perennial shrub common in Neotropical floodplains. It produces abundant EFNs and supports a diverse arthropod fauna, including both specialist and generalist herbivores, as well as multiple guilds of natural enemies (Keeler 1977; Frey 1995). Its widespread distribution and ecological role make it an ideal system to investigate community-level structuring of plant–arthropod interactions across diel cycles.

Therefore, our study aimed to describe the daily dynamics of herbivores and natural enemies associated with *I. carnea* in the Pantanal. Specifically, we asked: (i) how do natural enemy guilds (ants, spiders, wasps) partition their activity across the day–night cycle? (ii) how does herbivore occurrence vary in response to enemy presence? and (iii) what community-level patterns emerge from diel turnover? By integrating descriptive observations with statistical models, our study provides a natural history baseline to generate hypotheses for future experimental tests and contributes to understanding how temporal complementarity in enemy activity sustains continuous defense in a highly dynamic wetland ecosystem..

Material and Methods

Study area

We chose a natural population of *I. carnea* located in Pantanal on Estrada Parque, Ponte 14 (19º34'37"S, 57º00'42"W) in the vicinity of the Base de Estudos do Pantanal of the Universidade Federal de Mato Grosso do Sul, Corumbá, Mato Grosso do Sul, Brazil. *Ipomea carnea* has extrafloral nectaries (EFNs) that attract ants and other potential predators of herbivorous insects, such as wasps and spiders (Keeler 1977; Steward and Keeler 1988). According to Keeler (1977), *I. carnea* has two EFN systems: one located at the distal part of the leaf petiole and the other composed of a ring of five nectaries at the base of each flower, around the pedicel, which are visited by ants of different species (Fig. 1). The Pantanal in Mato Grosso do Sul state, Brazil, is a large humid area formed by the coalescence of the Paraguay River and its tributaries. It has a subsumed tropical climate of the A type (Alvares et al. 2013). The vegetation of the sedimentary plain is a mosaic of aquatic areas, flooded fields, riparian forests, savannas (cerrado), cerradão, deciduous forest, and a large part of savannas and monodominant pioneer formations such as the cotton formed by species of the genus *Ipomoea*, popularly known as wild cotton (Pott et al. 2011b). With accumulated precipitation data and the average monthly temperature of the sampled months, obtained from the CEMTEC-MS website (Centro de Monitoramento de Tempo, do Clima e dos Recursos Hídricos de Mato Grosso do Sul) for the Municipality of Corumbá, we constructed a climatic diagram to characterize the area during the months of study. According to the diagram, the region showed a dry and cold season (July–September), a wet and hot season (November–February), and a wet season with lower temperatures (March–July).

Arthropod sampling

Monthly collections were carried out from November 2012 to October 2013, in a population of *I. carnea*. Thirty individuals at a minimum height of 1.5 m from the ground and separated by a minimum distance of 5 m were chosen to cover the entire area for each monthly sampling. We recorded the number of herbivorous leaf insects and natural enemies (ants, wasps, spiders, and other arthropods) visiting extrafloral nectaries in three branches per individual. The specimens were identified by family and/or genus, and in some cases by species, using specialized literature (e.g.: Rafael et al. 2012; Baccaro et al. 2015). We also consulted specialists to confirm species identification (see acknowledgements). These records were performed in three periods: Daytime (8 a.m.–10 a.m.), afternoon (2 p.m.–4 p.m.), and nighttime (7 p.m. – 9 p.m.). On the other hand, herbivores were classified as specialists (*Charydotella rubicunda* and *Chellymorpha cribraria*) and generalists (the rest of the herbivores).

Data analysis

We used a descriptive and correlational approach to identify natural patterns in arthropod activity, which serves as a bias for generating hypotheses for future experimental studies. The occurrence (richness and abundance) of herbivores and natural enemies per plant (individual / plant) was organized by periods (morning, afternoon, and night). To verify the normality of the data, a Kolmogorov - Smirnov test was performed. One-way ANOVA was performed to compare the occurrence of herbivores and natural enemies between periods (daytime, afternoon, and night). To verify if the interaction of natural enemies with leaf herbivores, both in richness and abundance, is different among the period of the day, a Generalized Linear Mixed Model (GLMM) was used. To assemble this model, we verified the types of distribution in each analyzed set, using the package “ftdistrplus” (Delignette-Muller et al. 2010) with the Poisson Distribution being the most suitable for the database. The models (GLMM) and interactions were tested using the “glmer” function (Bates and Maechler 2010) considering each plant individual as a random factor. To verify whether the presence or absence of natural enemies is related to the occurrence of the main species of herbivores (specialists and generalists), we used the analysis of indicator species (Indval) considering the relative frequency of species and concentration of abundance in certain groups (absence and presence of natural enemies), using the package “Indicspecies” (De Cáceres 2013). These analyses were performed on the R platform (R Core Team 2021).

Results

Over one year of observations, we recorded 19,347 natural enemies and 1,996 herbivores associated with *Ipomoea carnea*. Ants were by far the most common enemies (71% of all records), followed by spiders (19%) and wasps (10%). Herbivores were more diverse, including a mix of generalists and two specialist taxa that were consistently observed feeding on leaves, often protected by frass or silk shelters.

Temporal dynamics of natural enemies

Natural enemy guilds exhibited clear diel turnover. Ants dominated the plants during morning and afternoon periods, reaching their lowest activity at night. Spiders, in contrast, were strongly nocturnal and represented the main predators after sunset. Wasps were less abundant overall, but their presence was concentrated during daylight hours (see full ANOVA outputs in Table S1a).. This temporal partitioning indicates that different groups of enemies alternate dominance over the daily cycle, maintaining continuous predation pressure on the plants (Fig. 2).

Temporal dynamics of herbivores

Herbivores also varied across the diel cycle, responding differently depending on their feeding strategy. Overall herbivore abundance and richness declined during the day when ant activity was highest. Specialist herbivores, which often display behavioral defenses against ants, became more frequent at night, when ants were less active. However, their abundance was lower in periods dominated by spiders, suggesting that nocturnal predation limits their activity. Generalist herbivores occurred throughout the cycle but tended to be less abundant during the afternoon, coinciding with higher wasp presence (model results in Table S1b). These patterns reveal that herbivore guilds respond differently to the temporal dynamics of their enemies.

Enemy–herbivore associations

Patterns of association between herbivores and natural enemies revealed guild-specific relationships. Ants were negatively related to both herbivore abundance and richness, particularly in daytime periods. Spiders were associated with reduced numbers of specialist herbivores at night, while wasps were negatively related to generalist herbivores during daylight (indicator species analysis in Table S1c). Together, these results support the hypothesis that complementary guilds of natural enemies exert time-specific control on herbivores (Table S1).

Community-level structuring

Indicator species analyses highlighted the strong temporal fidelity of both herbivores and their enemies. Specialist herbivores were disproportionately associated with nocturnal periods, whereas generalists occurred across all time windows. Ants were consistently linked to daylight, spiders to night, and wasps to afternoon activity. This turnover creates a “defense in shifts” dynamic in which different predator guilds replace one another over the diel cycle, resulting in nearly continuous top-down regulation of herbivores (Fig. 3).

Discussion

Our year-round observations of *Ipomoea carnea* in the Pantanal reveal clear daily patterns in the structure of associated arthropod communities. By surveying across morning, afternoon, and night, we documented that natural enemies partition their activity temporally, resulting in continuous pressure on herbivores. Ants were predominant during the day, spiders dominated at night, and wasps were most active during daylight. This temporal complementarity produced distinct associations with herbivores: ants coincided with reduced herbivore abundance and richness, spiders with lower occurrence of specialist herbivores at night, and wasps with modest but consistent reductions of generalist herbivores. These results confirm that different predator guilds contribute to herbivore control in complementary ways.

Temporal structuring of natural enemies

The temporal partitioning of ants, spiders, and wasps suggests that *I. carnea* benefits from a "defense in shifts", whereby different predator guilds exert pressure during different periods. Similar diel patterns have been observed in other systems, where ants dominate EFN interactions by day and spiders contribute at night (Oliveira & Del-Claro 2005; Yamawo et al. 2014; Lange et al. 2021). This complementarity may be driven by the differential preferences of these enemies for plant rewards: ants and spiders are often attracted by sugar-rich extrafloral nectar, while wasps can be rapidly recruited by volatile organic compounds released by plants (Röse et al. 2006; Pfannenstiel & Patt 2012; Alves-Silva et al. 2013). Thus, our findings expand current knowledge by documenting these complementary dynamics in a Neotropical wetland context.

Herbivore responses and guild-specific associations

Herbivores displayed guild-specific responses to enemy turnover. Specialists were most frequent at night, coinciding with reduced ant activity, but their numbers declined when spiders were abundant. This suggests that the defensive strategies of specialists, such as chemical camouflage or fecal shields, might be effective against ants and wasps but are circumvented by hunting modes of nocturnal spiders (Massuda & Trigo 2014). Generalists occurred throughout the day but tended to be less abundant in periods of high wasp activity. These guild-specific responses reinforce the idea that multiple enemy guilds act synergistically, creating a temporal mosaic of top-down effects (Snyder et al. 2006; Dáttilo et al. 2013).

Contributions to natural history and wetland ecology

Our findings highlight *I. carnea* as a focal species for understanding arthropod community dynamics in wetlands. EFNs serve as keystone resources that structure communities across trophic levels (Heil & McKey 2003; Rico-Gray & Oliveira 2007; Silva-Viana et al. 2021). The plant itself may actively mediate this temporal structuring; evidence from other systems shows that plants can modulate extrafloral nectar secretion, both in quantity and quality, across the diel cycle to attract specific defenders when most needed (Romero & Izzo 2004; Radhika et al. 2010; Falcão et al. 2014). By documenting how these interactions unfold across daily cycles, our study expands the scope of EFN ecology beyond diurnal observations. In the Pantanal, where seasonal flooding and habitat heterogeneity strongly influence plant–arthropod interactions (Junk et al. 2006; Tomas et al. 2019; Meurer et al. 2015; Yamazaki et al. 2016), such temporal structuring may be particularly important for maintaining ecological stability.

Therefore, daily turnover should be considered an additional axis of variation shaping wetland arthropod communities.

Limitations and future perspectives

While our results demonstrate strong temporal patterns, they remain correlative. We did not manipulate EFN availability or exclude predator groups and therefore cannot infer direct causal effects of enemies on herbivores or plant fitness. Future experimental approaches, such as predator-exclusion assays, manipulations of nectar availability, or time-series analyses such as empirical dynamic modeling (Sugihara et al. 2012), could test the hypotheses generated here. Nevertheless, descriptive studies like ours are essential for identifying the natural history patterns that underpin experimental design and for capturing ecological dynamics that might otherwise remain unnoticed. We emphasize that such baselines are especially critical in ecosystems undergoing rapid environmental change.

Final remarks

By documenting daily turnover in arthropod communities associated with *I. carnea*, we provide rare evidence of temporal complementarity among natural enemies in a wetland ecosystem. These findings also carry applied relevance: diel interactions are likely sensitive to hydrological alterations and fire, two of the major emerging threats to the Pantanal (Tomas et al. 2019; Leal Filho et al. 2021; Arruda et al. 2022). Beyond their intrinsic ecological value, such baselines are critical for conservation, as they reveal how species interactions are structured in one of the world's most threatened wetlands. Our work thus offers both ecological insights and practical references for monitoring how intricate interaction networks respond to ongoing disturbances in the Pantanal.

Declarations

Ethical approval:

For this type of study formal consent is not required.

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Conflict of Interest: The authors declare that they have no conflict of interest.

Author Contributions:

MOCN and JRT contributed to the study conception and design. Material preparation and data collection were performed by MOCN. The first draft of the manuscript was written by MOCN, JRT and REV commented on previous versions of the manuscript. MOCN, JRT and REV read and approved of the final manuscript.

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Availability of data and material:

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Figures

Figure 1

Ipomoea carnea in the wetland. Highlight in the presence of extrafloral nectaries at the base of leaves and flowers (EFN). Photos: Milton O. Cordova

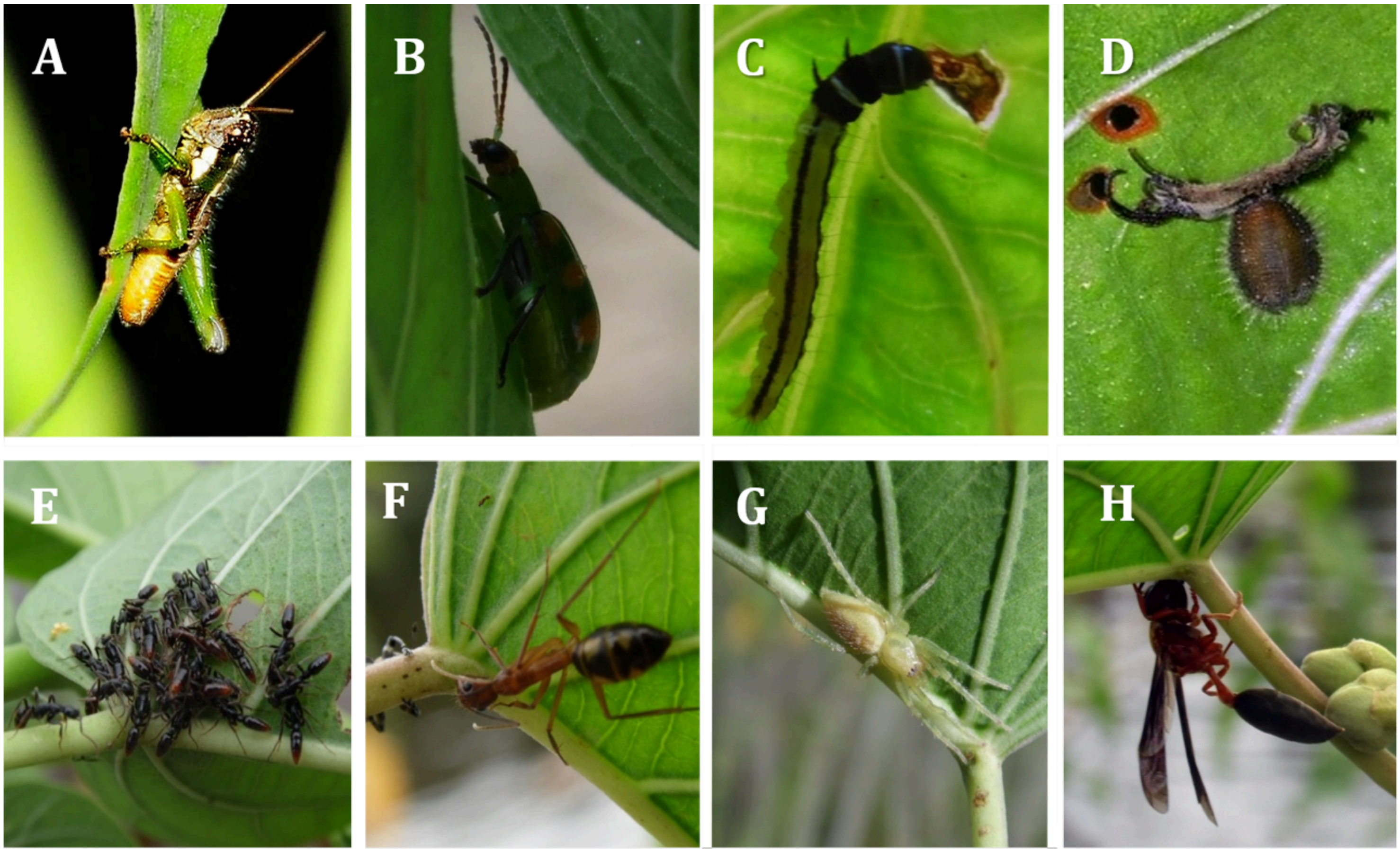

Figure 2

Representatives of herbivores (A-D) and natural enemies (E-H) on *Ipomoea carnea* in the Brazilian Pantanal. A. *Schistocerca* sp. (Acrididae, Orthoptera), B. *Diabrotica*sp. (Chrysomelidae, Coleoptera), C. Tortricidae larvae (Lepidoptera), D. *Chellymorpha cribaria* larvae (Chrysomelidae, Coleoptera), E. *Leptogenys* sp. (Formicidae, Hymenoptera), F. *Camponotus* aff. *melanoticus* (Formicidae, Hymenoptera), G. Araneidae (Arachnida), H. *Polistes* aff. *major* (Vespidae, Hymenoptera). Photos: Milton O. Cordova

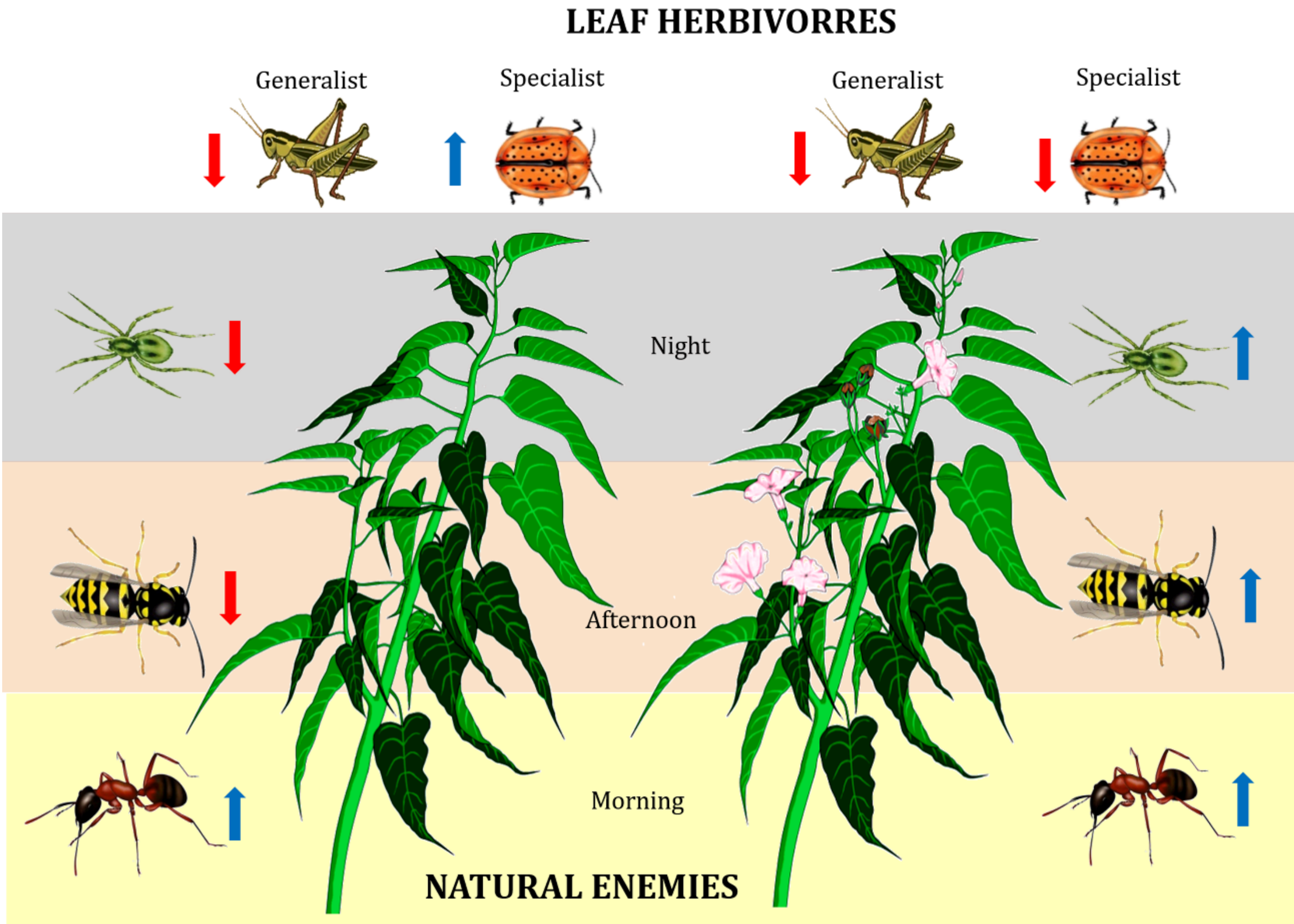

Figure 3

Role of period of the day in the behavior of leaf herbivores and natural enemies in the vegetative and reproductive stages of *Ipomoea carnea* in the Pantanal (Illustration: Milton O. Cordova)

Supplementary Files

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- SupplementaryTableS1.docx