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Trophic roles of scavenger beetles in relation to decomposition stages and seasons

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ABSTRACT

Carcasses represent a trophic and reproductive resource or shelter for arthropods, which are a representative component of the decomposition process. Four experiments, one per season, were conducted in a semi-rural area of Bahía Blanca, Argentina, to study the trophic roles of cadaveric beetles, evaluating the abundance, composition and dominance during all decomposition stages and seasons. Species of necrophagous, necrophilous and omnivorous habits were found. Abundance, composition and dominance of beetles in relation to their trophic roles changed according to seasons and decomposition stages. Guilds and patterns of succession were established in relation to those periods. Trophic roles could be an indicator of beetle associations with decomposition stages and seasons.

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Introduction

Carcasses represent a trophic and reproductive resource or shelter for a variety of animals such as arthropods, which are a representative component of the decomposition process. Leclercq (1974) proposed an ecological classification based on the trophic roles of the cadaveric fauna: necrophages (feed from corpses), necrophiles (predate on or parasitize other arthropods), omnivores (feed from corpses and predate on other arthropods) and incidentals (look for refuge or appear at random). The carrion arthropod community is mainly represented by insects (Carvalho et al., 2000). These are capable of detecting chemical changes, so their appearance in one particular stage of decomposition is not likely to be accidental (Magaña, 2001; Archer and Elgar, 2003; Dekeirsschieter et al., 2011; Von Hoermann et al., 2011, 2012). Segura et al. (2011) suggested that decomposition stages are a primary factor in determining the insect community, because the species exhibit adaptations that allow them to exploit and use corpses under different conditions and periods of time.

The decomposition process and the cadaveric fauna succession can be influenced by circumstances that cadavers go through after death and many variables have to be considered in each situation: climatic conditions, season, geographical region, sun exposure, synanthropy, latitude, substrate type, larval migration,

amongst others (Greenberg, 1971; Catts and Goff, 1992; Goff, 1992; Kócarek, 2001; Centeno et al., 2002; Forbes et al., 2005; Faria et al., 2007; Battán Horenstein and Linhares, 2011; Dekeirsschieter et al., 2011; Matuszewski et al., 2014). Thus, the study of these variables is important for the estimation of postmortem interval (PMI) and other applications in forensics (Keh, 1985; Anderson, 2001; Centeno et al., 2002; Dourel et al., 2010; Battán Horenstein and Linhares, 2011; Ortloff et al., 2012; Pers. comm., Zanetti et al., 2015).

Beetles are especially useful in forensic cases in which Diptera have not been sampled or when they have already left the body and only beetles can be found (Centeno et al., 2002). But also, some species of Coleoptera have been observed in earlier stages of decomposition and they can appear in different waves in a body, thus, further studies on this order need to be conducted.

The aim of this study was to analyze the abundance, composition and dominance of cadaveric beetles per season and decomposition stage in accordance with their trophic roles (guilds).

Materials and methods

This study is a part of a greater study of decomposition and cadaveric succession (Pers. comm., Zanetti et al., 2015). The experiments were carried out in a field property of the Universidad Nacional del Sur, located at Bahía Blanca (38°41′41″ S, 62°15′10″ W), Buenos Aires province, Argentina.

Twelve domestic pigs (*Sus scrofa* L.) weighing 15–16 kg were used. Three of them were killed each season by a stab to the heart (the usual procedure of commercial butchers) 1 h before exposure,

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and were kept inside a plastic bag to keep away insects until the beginning of the experiment. The Ethical Commission of the Universidad Nacional del Sur approved this procedure. Each carcass was laid inside a cage to protect it from scavenger vertebrates, and under direct sun along transects separated 100 m from each other. To complement the sampling, six pitfall traps were placed around each cage at a distance of 50 cm from the carcass (experimental traps); two per each long side and one per each wide side. For control purposes, other six pitfall traps with the same spatial pattern were placed at 15–30 m from the last cage.

Literature typically refers to decomposition as a process of five stages that are not necessarily discrete (Bornemissza, 1957; Schoendly and Reid, 1987; Moura et al., 2005) but which can be used as a guide or reference points. We followed the criterion established by Centeno et al. (2002) to define the stages of decomposition. Carcasses were visited daily until concluding the experiment (several days after the carcass reached the remains stage). Beetles from on, under and inside the corpses were collected manually with entomological forceps. Beetles were taken from cadavers (per day) only if 10% of the individuals (this percentage was considered for each family) were available in order to avoid any alteration in the decomposition and/or succession processes due to loss of insects, and preserved into plastic containers with ethanol 70%. Some larvae were reared for identification of the specimens and cultures with adults were established for future research (Pers. comm., Zanetti et al., 2015). Taxonomical determination or corroboration of some species/morphospecies was performed by some specialists. The specimens were deposited dry-mounted or in alcohol at Cátedra de Zoología de Invertebrados II, Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur.

Species and morphospecies were grouped in accordance with their trophic roles. Firstly, we evaluated the composition and abundance of each group, calculating the mean and SE of each one per sampling unit (observations and/or capture on carcass or capture in six pit fall traps) and day, during each season and decomposition stage. Secondly, we analyzed the dominance of each group.

Results

Beetles of necrophagous, necrophilous and omnivorous habits were found. Tables 1–3 show the species/morphospecies that were detected.

Table 2
Species/morphospecies of necrophagous habits.

Families	Species/morphospecies
Dermestidae	*Dermestes maculatus* (De Geer, 1774)
Tenebrionidae	*Scotobius clathratus* (Guérin-Méneville, 1834)
	Scotobius miliaris (Billberg, 1815)
	Scotobius muricatus (Guérin-Méneville, 1834)
Scarabaeidae	*Aphodius militaris* (LeConte, 1858)
	Aphodius pseudolividus (Balthasar, 1941)
	Ataenius platensis (Blanchard, 1844)
	Canthon ornatus bipunctatus (Burmeister, 1873)
	Degallieridium sp.
	Pseudocanthon sp.
	Onthophagus sp.
Trogidae	*Omorgus batesi* (Harold, 1872)
	Polynoncus gemmingeri (Harold, 1872)

Table 3
Species/morphospecies of omnivorous habits.

Families	Species/morphospecies
Anthicidae	Anthicidae sp.
Cleridae	*Necrobia rufipes* (De Geer, 1775)
Nitidulidae	*Nitidula carnaria* (Schaller, 1783)

Abundance of guilds

Necrophiles

It was the most abundant group. More than 38 species were observed. In cadavers, in order of frequency and abundance, they were Carpelimus spp., Aleocharinae spp., *Philonthus flavolimbatus* (Erichson, 1753), *Creophilus maxillosus* (Linnaeus, 1758) (Staphylinidae); *Euspilotus (Hesperosaprinus) pavidus* (Erichson, 1834), *Phelister* sp., *Euspilotus* (sensu stricto) *ornatus* (Blanchard, 1843), *Euspilotus* (sensu stricto) *lacordairei* (Marseul, 1855) and *Euspilotus* (sensu stricto) *patagonicus* (Blanchard, 1843) (Histeridae); while in traps, *Hylitus tentyroides* (Lacordaire, 1830) (Tenebrionidae) and the tribes Harpalini, Cyclosomini, Lebiini, Pterostichini, Bembidiini (Carabidae) were the most representative. In Fig. 1A and B the mean abundance of necrophiles per decomposition stage and season according to the sampling method is presented. This group was more abundant in spring and summer. During spring, the abundance was greater in Advanced Decay, and in summer there were more individuals in Active Decay followed by Advanced Decay. In traps, the group showed a similar behavior

Table 1
Species/morphospecies of necrophilous habits.

Families	Species/morphospecies	Families	Species/morphospecies
Archeocrypticidae	*Archeocrypticus topali* (Kaszab)	Histeridae	*Phelister* sp.
Melyridae	*Astylus* sp.		*Xerosaprinus (X) diptychus* (Marseul)
Carabidae	*Pelmatellus egenus* (Dejean)		Dendrophilinae spp.
	Bradycellus viduus (Dejean)		Histerinae sp. 1
	Selenophorus (S) punctulatus (Dejean)		Histerinae sp. 2
	Tetragonoderus chalceus (Chaudoir)	Tenebrionidae	*Blapstinus punctulatus* (Solier)
	Tetragonoderus laevigatus (Chaudoir)		*Gondwanocripticus platensis* (Fairmaire)
	Carbonellia platensis (Berg)		*Hylitus tentyroides* (Lacordaire)
	Argutoridius oblitus (Dejean)		*Leptynoderes strangulata* (Fairmaire)
	Notaphus posticalis platensis (Negre)		*Trichoton roigi* (Ferrer and Moragues)
Histeridae	*Carcinops* sp.	Scarabaeidae	*Archophileurus chaconus* (Kolbe)
	Euspilotus sp.		*Archophileurus fodiens* (Kolbe)
	Euspilotus (H) caesopygus (Marseul)	Staphylinidae	Aleocharinae spp.
	Euspilotus (H) connectens (Paykull)		*Carpelimus* spp.
	Euspilotus (ss) lacordairei (Marseul)		*Creophilus maxillosus* (Linnaeus)
	Euspilotus (H) niger (Arriagada)		*Haematodes* sp.
	Euspilotus (ss) ornatus (Blanchard)		*Haematodes bicolor* (Laporte)
	Euspilotus parenthesis (Schmidt)		*Philonthus flavolimbatus* (Erichson)
	Euspilotus (ss) patagonicus (Blanchard)		
	Euspilotus (H) pavidus (Erichson)		

Fig. 1. Mean abundance (±SE) of necrophilous beetles per decomposition stages and seasons. (A) Cadavers (c). (B) Traps (st). F, Fresh; B, Bloated; ACD, Active Decay; ADD, Advanced Decay; R, Remains.

Fig. 2. Mean abundance (±SE) of necrophagous beetles per decomposition stages and seasons. (A) Cadavers (c). (B) Traps (st). F, Fresh; B, Bloated; ACD, Active Decay; ADD, Advanced Decay; R, Remains.

as in cadavers, but the abundance increased from Bloated stage to Advanced Decay.

Necrophiles were also found as inmatures. We observed larvae belonging to Histeridae, Staphylinidae, Tenebrionidae and Carabidae.
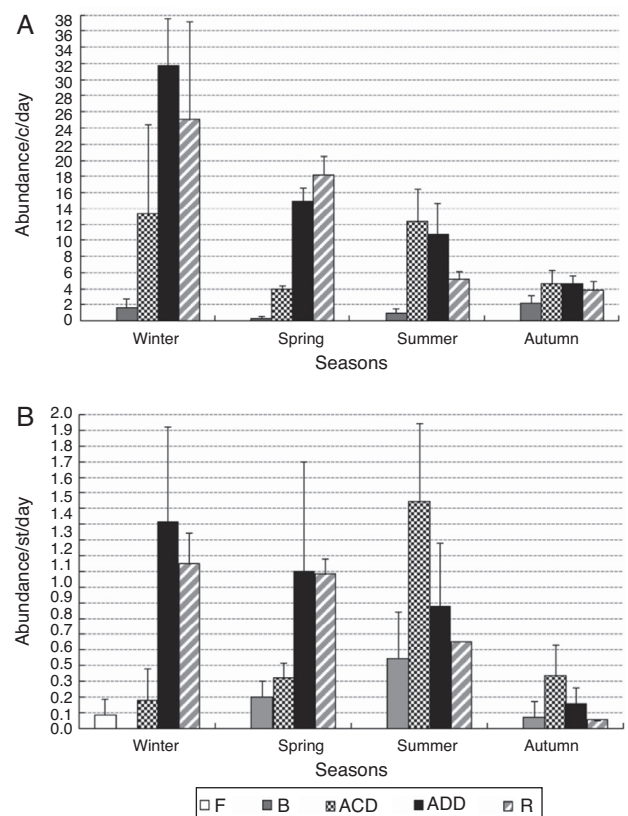
Necrophages

There were found 13 species. *Dermestes maculatus* (De Geer, 1774) (Dermestidae) was the most abundant in all seasons. This species was followed, in order of frequency and abundance in cadavers, by *Polynoncus gemmingeri* (Harold, 1872) (Trogidae); *Scotobius muricatus* (Guérin-Méneville, 1834) (Tenebrionidae); *Onthophagus* sp. and *Canthon ornatus bipunctatus* (Burmeister, 1873) (Scarabaeidae); while in traps, *Scotobius miliaris* (Billberg, 1815) (Tenebrionidae); *Aphodius pseudolividus* (Balthasar, 1941) and *Ataenius platensis* (Blanchard, 1844) (Scarabaeidae) were the most representative. Fig. 2A and B shows the mean abundance of necrophages along the decomposition process during each season and considering the sampling method. This group was more abundant in winter and this season was characterized by an increase in the number of individuals from Bloated stage to Advanced Decay. In spring, necrophages showed a similar pattern as in winter, but with the difference that the abundance did not decrease in Remains. In traps, Advanced Decay and Remains were the most abundant stages during winter and spring. Instead in summer, specimens were more abundant in Active Decay.

In addition to the necrophagous adults, we collected larvae of *Dermestes maculatus* and Scarabaeidae.

Omnivores

Three species were observed in cadavers: *Nitidula carnaria* (Schaller, 1783) (Nitidulidae) and *Necrobia rufipes* (De Geer, 1775)

(Cleridae) were more representative in abundance and frequency, while in traps was Anthicidae sp. In Fig. 3A and B the mean abundance per decomposition stage and season according to the sampling method is illustrated. This group was more abundant in summer and during this season, the number of specimens was greater in Advanced Decay and Active Decay. During spring, there were more specimens in the last two stages and in summer, the Advanced Decay showed a notable increase.

As with the other guilds, we found inmatures. In this case, larvae belonged to *Nitidula carnaria* and *Necrobia rufipes*.
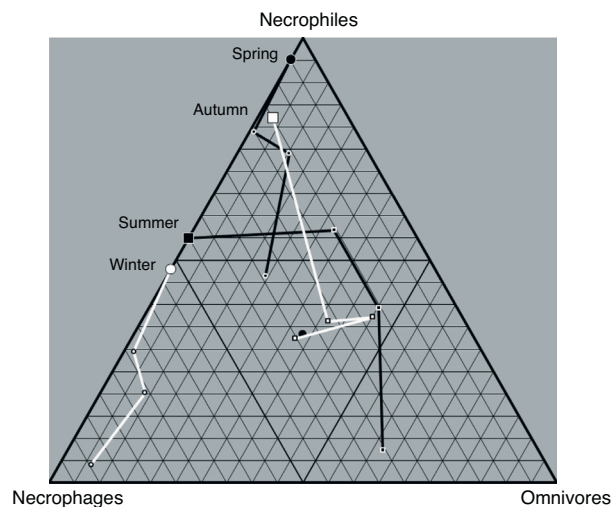
Dominance of guilds

The dominance of beetle guilds was analyzed and the results are shown in Fig. 4. In winter, necrophages was the dominant guild. Their relative frequency was high during all the decomposition process, increasing from the Bloated stage (52%) until Remains (90%). At the same time, the proportion of necrophiles decreased and omnivores appeared. During spring, necrophiles constituted the most representative guild. The dominance of this group decreased from the Bloated stage (95%) until Remains (46%). In summer, proportions were similar between the three groups. The Bloated stage was represented by necrophiles (55%) followed by necrophages (45%). In Active Decay, necrophiles continued dominate (57%), while at the same time the presence of necrophages decreased notably (15%) and appeared omnivores (28%). In Advanced Decay, omnivores became dominant (45%) and were followed by necrophiles whose presence decreased (39%). In Remains, the greater relative frequency of the population was represented by omnivores, with an increase in their values (62%), while necrophiles decreased notably (7%) and necrophages increased (31%). During autumn, necrophiles showed a greater proportion; the other groups were almost in equal proportions. The relative
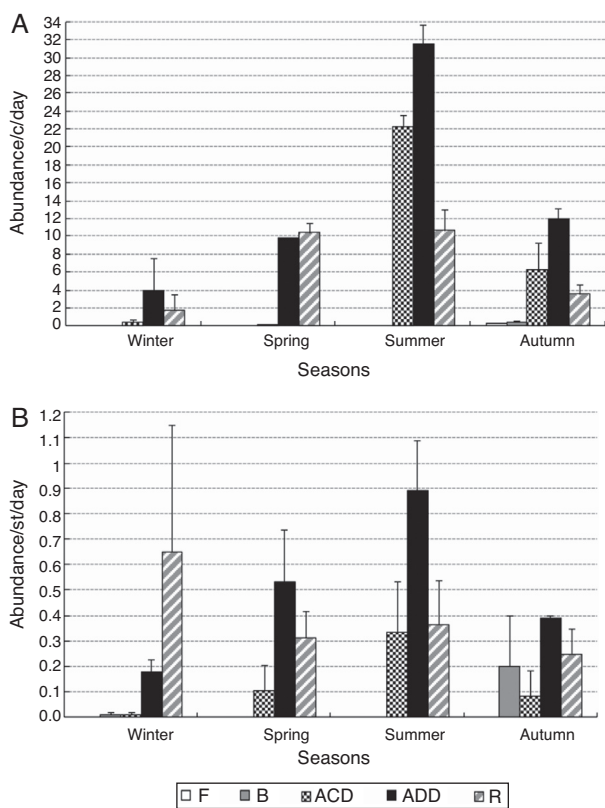
Fig. 3. Mean abundance (±SE) of omnivorous beetles per decomposition stages and seasons. (A) Cadavers (c). (B) Traps (st). F, Fresh; B, Bloated; ACD, Active Decay; ADD, Advanced Decay; R, Remains.

Fig. 4. Dominance of beetle guilds observed in cadavers per decomposition stages and seasons, represented in a ternary diagram. Each line of the sides of the triangle is equal to a 5% of the total. The black point corresponds to the equicomposition (33.3% for each guild). The greater point in each line indicates the initial decomposition stage per season.

frequency of necrophiles was maximum in the Bloated stage (82%) and then decreased in Active Decay (36%), in the other stages there was no variation. The proportion of necrophages and omnivores was more or less constant between stages; with the difference that the relative frequency of omnivores was greater than necrophages and they scarcely appeared in the Bloated stage.

In Fig. 5A and D are present the results of dominance of beetles captured in traps. Necrophiles were the predominant guild during the four seasons and through the decomposition process. During winter, necrophiles dominated during all the process. While the proportion of this group decreased, necrophages and omnivores became notable, particularly toward Remains. In the other seasons, necrophiles also predominated, but their importance did not decrease toward the end of the process.
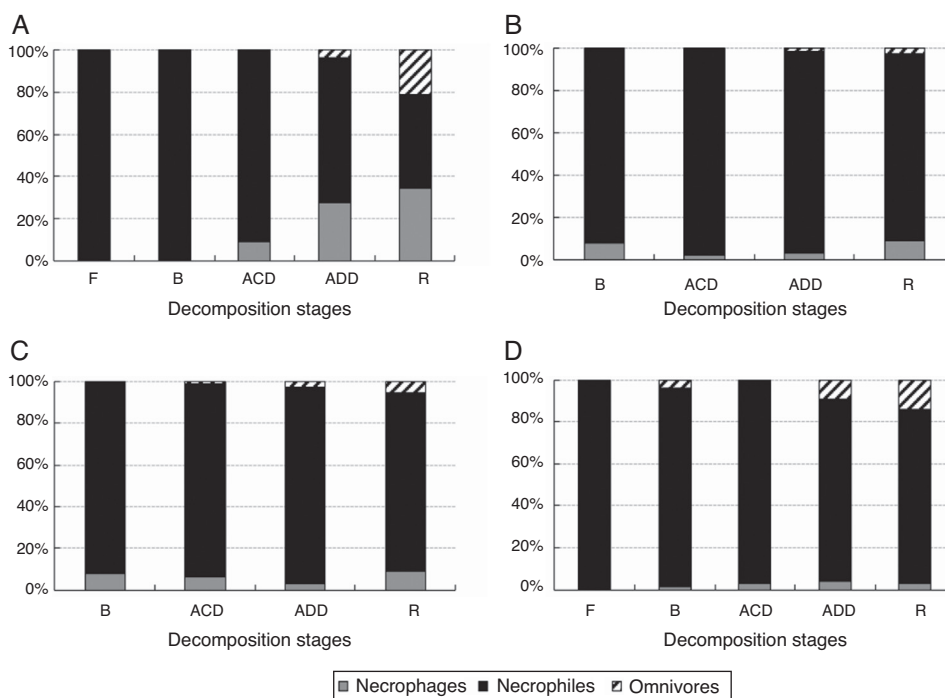
Fig. 5. Dominance of beetles guilds captured in traps per decomposition stage and seasons. (A) Winter. (B). Spring. (C). Summer. (D). Autumn. F, Fresh; B, Bloated; ACD, Active Decay; ADD, Advanced Decay; R, Remains.

Discussion

In cadavers, specific dominance changed according to seasons and decomposition stages. We inferred that during winter to the extent that decomposition process progressed, necrophages became dominant and omnivores appeared, while the proportion of necrophiles decreased. In spring, when the dominance of necrophiles started to diminish, the other groups appeared, having necrophages a greater representation than omnivores. During summer, the decrease of necrophiles seems to contribute to a greater relative frequency of omnivores. This succession could be a result of temporal segregation as a form of reducing overlapping, depredation or competition for food resources (Zanetti, 2013).

We observed some relations between the length of each stage of decomposition and the presence of species. These relations were mostly observed in winter: *Carpelimus* spp. and Aleocharinae spp. were more frequent in Active and Advanced decay than Bloated stage; *E. (Hesperosaprinus) pavidus* and *N. carnaria* were more frequent in Advanced Decay and Remains than in the others stages; *Phelister* sp. and *E. (sensu stricto) ornatus* were more frequent in Advanced Decay than in Remains; and *E. (sensu stricto) patagonicus* only appeared in Advanced Decay. Some relation was also observed in spring with *S. muricatus*, which was more frequent in Remains than in Bloated stage; and *A. pseudolividus* was only found in Remains. *Ataenius platensis* was only found in Advanced Decay in winter and in Remains during summer (Pers. comm., Zanetti et al.). Considering these findings, the length of each decomposition stage not always is a determining factor per se, instead several factors could act in combination.

These results contraposed with those reported by Arnaldos et al. (2005) who mentioned that omnivores appeared at the same time that necrophiles, maintaining through decomposition stages. Iannacone (2003) described that necrophages were more abundant and with a greater number of species, and were followed by necrophiles. Instead, the opposite happened in the actual study. These differences could be attributed to a variety of causes, such as geographical region, climatic conditions, species, type and size of the carcass, location of the cadaver, study area, methodology used, amongst others.

The strong association of dermestids (necrophages) with winter could be related to a lesser presence of dipteran larvae and to a longer decomposition process, which could provide more cadaveric tissues during more time, not only for feeding but also for reproducing (Pers. comm., Zanetti et al., 2015). In this way, more dipteran larvae could consume a greater cadaveric biomass, reducing the food availability for dermestids or other necrophages, meanwhile such larvae could favor the presence of necrophiles such as rove beetles, clown beetles or carabids, which are predators of them and other insects in different stages of development (Pers. comm., Zanetti et al., 2015), and some are parasites of dipteran puparia (Ashe, 2002; Mise et al., 2010). The appearance of necrophiles indicates the existence of necrophagous fauna already installed in the cadaver (Catts and Goff, 1992) and the frequency of necrophiles is directly related with the presence of the prey. Since the preys of necrophiles are usually dipteran larvae (Fichter, 1949), it is expected that the frequency of necrophiles decreases with the biomass loss and the reduction of the dipteran larvae. Because omnivores can act as predators, it can be expected that they coexist in a lesser degree with necrophiles, but frequently with necrophages because they can feed on them and like them, they can use a carcass as a food resource. Clerids dominated when the frequency of rove and clown beetles decreased (Pers. comm., Zanetti et al., 2015). With respect to certain authors, nitidulids arrive in later stages of decomposition sharing with dermestids (Payne and King, 1969; Olaya Másmela, 2001; Özdemir and Sert, 2009). Thus, it could happen that both, the absence or low frequency of a guild,

and the stage of decomposition, could influence the abundance and dominance of certain group.

Coprophagous beetles (scarab beetles) were observed in the study but they were considered as part of the necrophagous group due to the facultative capacity of these beetles such as feeding from tissues.

Conclusion

Differences in the abundance and dominance of beetles in accordance with their trophic roles (guilds) were found per season and decomposition stages. There is an association between these periods and the feeding habits of beetles, as a succession. The necrophiles (principally rove beetles) dominated between early stages, sharing this with necrophages (particularly dermestids) in winter. The necrophages were the dominant guild during winter principally in the last two stages. The omnivores showed a major dominance in summer during Advanced Decay and Remains.

Just as the arthropod succession is usually used in the estimation of PMI (generally a maximum PMI), the results reported in this work underline that knowing or establishing what guild was present or absent and when the same prevailed, can be of relevance in evaluating important alterations in succession which could indicate abnormal conditions in the decomposition of the cadaver, particularly in the region where our study was conducted. Also, knowing how the guilds behave, for example, the appearance of necrophiles indicates the existence of necrophagous fauna already installed in cadavers, should be considered when examining the crime scene and collecting entomological evidence, as well as to avoid errors and in the estimation of PMI.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgments

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