

**PAPER****PATHOLOGY/BIOLOGY**

Noelia I. Zanetti,<sup>1,2</sup> Ph.D.; Elena C. Visciarelli,<sup>2</sup> Ph.D.; and Nestor D. Centeno,<sup>1</sup> Ph.D.

## Associational Patterns of Scavenger Beetles to Decomposition Stages

**ABSTRACT:** Beetles associated with carrion play an important role in recycling organic matter in an ecosystem. Four experiments on decomposition, one per season, were conducted in a semirural area in Bahía Blanca, Argentina. Melyridae are reported for the first time of forensic interest. Apart from adults and larvae of Scarabaeidae, thirteen species and two genera of other coleopteran families are new forensic records in Argentina. Diversity, abundance, and species composition of beetles showed differences between stages and seasons. Our results differed from other studies conducted in temperate regions. Four guilds and succession patterns were established in relation to decomposition stages and seasons. Dermestidae (necrophages) predominated in winter during the decomposition process; Staphylinidae (necrophiles) in Fresh and Bloat stages during spring, summer, and autumn; and Histeridae (necrophiles) and Cleridae (omnivores) in the following stages during those seasons. Finally, coleopteran activity, diversity and abundance, and decomposition rate change with biogeoclimatic characteristics, which is of significance in forensics.

**KEYWORDS:** forensic science, decomposition, cadaveric succession, carrion fauna, forensic entomology, Argentina

Corpses represent a trophic and reproductive resource for a variety of animals, with arthropods being a representative component of the decomposition process. Consequently, an ecological classification based on their trophic roles can be made: necrophages (feed from corpses), necrophiles (predate on or parasitize other arthropods), omnivores (feed from corpses or predate on other arthropods), and incidentals (look for refuge or appear at random) (1). The carrion arthropod community is represented mainly by insects (2). Among holometabola insects, Diptera and Coleoptera are orders of great importance. Some families of Coleoptera that are important in forensic entomology are Silphidae (necrophages and necrophiles); Staphylinidae and Histeridae (necrophiles); Trogidae, Dermestidae (necrophages); and Cleridae and Nitidulidae (omnivores) (3).

Payne (4) and Jirón and Cartín (5) observed that when vertebrate scavengers are absent, decomposition is faster in the presence of insects. These arthropods are capable of detecting chemical changes (6), so their appearance in one particular stage of decomposition is not likely to be accidental (7). Indeed, Segura et al. (8) have shown that decomposition stages are a primary factor in determining the insect community, because the different species exhibit adaptations that allow them to exploit and use corpses under different conditions and periods of time.

Studies of carrion succession provide several data such as species diversity, richness, abundance, the stages of development,

and the number of individuals of each stage of development (9,10). When these studies are carried out, it is necessary to consider that both the decomposition process and the succession of cadaveric fauna can be influenced by circumstances that corpses suffer after death. Many variables have to be taken into account in each situation: climatic conditions, season, geographic region, exposure to solar radiation, synanthropy, substrate type, latitude, altitude, location and position of the body, body size, cause of death, presence of clothes, intra- and interspecific competition, and larval migration, among others (6,11–17). Thus, the study of these variables is important for the estimation of postmortem interval (PMI) and other applications in forensics (13,16,18,19).

Beetles are particularly useful in forensic cases in which Diptera have not been obtained in samplings or when they have already left the body and only beetles can be found (16,17). Furthermore, some species of Coleoptera have been observed in earlier stages of decomposition and they can appear in different waves in a body; therefore, further studies on this order need to be conducted.

Because there is usually uniformity in the trophic roles and habits of species belonging to a particular family of the cadaveric community and studies in the temperate region and other regions of Argentina are still scarce (17,20,21), we aimed to describe and analyze the composition, abundance, and diversity of cadaveric beetles at the family level, including also an analysis at the species level. We also intended to establish possible colonization patterns of beetles and their association with decomposition stages in vertebrate corpses, as well as with the rest of the cadaveric fauna, in a semirural area in the temperate region of Argentina.

### Materials and Methods

The experiments were carried out in a field (property of the Universidad Nacional del Sur), located at Bahía Blanca

<sup>1</sup>Laboratorio de Entomología Aplicada y Forense, Departamento de Ciencia y Tecnología, Universidad Nacional de Quilmes, Sáenz Peña 352, Bernal 1876, Provincia de Buenos Aires, Argentina.

<sup>2</sup>Cátedra de Parasitología Clínica, Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur, San Juan 670, Bahía Blanca 8000, Provincia de Buenos Aires, Argentina.

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(38°41'41"S; 62°15'10"W), Buenos Aires Province, Argentina. The selected area can be described as semirural. The vegetation was represented by graminoids, *Chenopodium quinoa* subsp. *Melanosperrum*, *Eucaliptus globulus*, *Populus alba*, *Prosopis alptaco*, and *Tamarix* sp. The climate is temperate, subhumid with moderate temperature and high variability throughout the year. According to the classification established by Köppen, it may be considered "pampeano" (a variation of the subtropical wet climate) because the average temperature can be higher than 22°C in warm months and there is no dry season (22). It differs from other zones with wet subtropical climate because of the minor annual thermic oscillation that is produced, therefore presents warmer summers which are also the rainiest and soft winters where snowfalls are rare. (22). Winters are cold with frosts, having the average maximum and minimum temperatures, 16.5 and 3.8°C, respectively. In spring, the average maximum and minimum temperatures are 26.1 and 21.1°C, respectively. In summer, temperatures can reach 40°C or even more and the minimum can keep high at night. The average maximum and minimum temperatures are 29.4 and 14.9°C, respectively. In autumn, they are 18.1 and 6°C, respectively. The average temperatures were calculated from data provided by the CERZOS-CONICET weather station located 2 km from the experimental area. The average relative humidity is 68% and the average annual rainfall is 600 mm, although there are important variations in the area, with rains being scarce in winter. Winds from the north and northeast predominate in summer and from the south and southeast in winter.

For each experiment (one per season, beginning in winter of 2010 and finishing in spring of 2011), three cages measuring 120 cm × 80 cm × 60 cm were built with wood and wire mesh of 2 cm pore wide to exclude vertebrate scavengers. Cages were placed under direct sun along transects, separated 100 m from each other. In total, twelve domestic pigs *Sus scrofa* L. of 15–16 kg weight were used. These animals were killed by a stab to the heart (the usual procedure of commercial butchers) 1 h before exposure and were kept inside a plastic bag, at ambient temperature (Table 1) and shadow, 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 on a wire mesh floor. 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. Other six pitfall traps with the same spatial pattern were placed at 15–30 m from the last cage for control purposes.

Literature typically refers to decomposition as a process of five stages that are not necessarily discrete (23,24), but which can be used as a guide or reference points. We followed the criterion established by Centeno et al. (16) to define the stages of decomposition. Carcasses were visited daily until concluding the experiment (several days after the carcass reached the Remains stage). The first sampling was carried out 24 h after placing the

carcasses, between 9 and 12 AM. Beetles from on, under, and inside the corpses were collected manually with entomological forceps. The relative humidity, minimum and maximum temperatures of each cadaver (measured by inserting a HT05 digital thermo-hygrometer probe into the anus) and from ambience were recorded. Meteorological information during the assays was provided by the CERZOS-CONICET weather station located at approximately 2 km from the study area. Beetles were taken from cadavers when 10% of the total individuals were available, to avoid any alteration in the decomposition and/or succession processes due to loss of insects, and preserved in plastic containers with ethanol 70%. Rearing was performed for identification of the specimens and also for future research. The specimens were deposited in the Cátedra de Parasitología Clínica, Universidad Nacional del Sur.

For the statistical analysis of general data, information was grouped according to decomposition stage. To incorporate summer, a F + B stage was defined as the sum of Fresh (F) and Bloated (B) stages, because in Fresh stage, individuals were not observed or captured during that season. The variables considered were the total number of cadaveric coleopterans per carcass and day, and the species diversity, for which the Shannon index (H) was used, in a Napierian logarithm scale. To establish whether seasons and stages (principal and second factors, respectively) influenced the variables mentioned above, we performed two-way ANOVA tests using InfoStat 2012p version (FCA—Universidad Nacional de Córdoba, Argentina). Pairwise comparisons were made with DMS at 5%. Also these tests and comparisons were performed to analyze the half abundance of each family and the influence that the seasons and stages could have on them. For these comparisons, we applied the same statistical probes used for general data, but when the variables exhibited many of zeros, descriptions of results had to be made. The same criterion was applied for statistical tests used for traps, differing in the sampling unit (observations on or under the carcass and accumulated capture in the six pitfall traps, respectively).

We carried out a multivariate analysis of principal components based on the covariance matrix between insects, using adult beetles, to explore in greater detail the relationship between the insects, the decomposition stages, and seasons. For this analysis, the information was grouped by stages and seasons. For this purpose, we used a database created with InfoStat 2012p version (FCA—Universidad Nacional de Córdoba, Argentina), in which the variable was the proportion of cadaveric beetles from each family per season and decomposition stages; families whose maximum contributions to composition never exceeded 15% were grouped into "Others". For the same reasons as was previously explained in relation to the other analysis, the Fresh (F) stage was combined with the Bloated (B) stage into the F + B stage. The groups formed in the multivariate analysis were obtained by performing a hierarchical cluster using Euclidean distance.

## Results and Discussion

The winter assay was prolonged into spring months. The speed of decomposition increased as the seasons became warmer, as was expected. Rodríguez and Bass (25) indicated that in cold seasons, the process of decomposition is slower because of a lesser degree of activity and abundance of insects. During winter, one of the carcasses needed more time to progress to Remains (24 days). This could be related to differences in the

TABLE 1—Ambient temperatures (°C) at which pig cadavers were kept inside the plastic bags 1 h before exposure, during each experiment.

Seasons	Temperature
Winter	13.6
Spring	14.6
Summer	28.5
Autumn	19.5

TABLE 2—Duration (Mean  $\pm$  SE) of each decomposition stage and of the whole process per season, expressed in days.

Seasons	Stages of decomposition					Total
	Fresh	Bloat	Active Decay	Advanced Decay	Remains	
Winter	7	19.3 $\pm$ 6.36	29.7 $\pm$ 0.33	80 $\pm$ 7.37	31 $\pm$ 5.86	167 $\pm$ 7
Spring	<1	5.7 $\pm$ 0.33	6.33 $\pm$ 0.33	5	20	38
Summer	<1	3	3	3	20	30
Autumn	1	5	4	41	20	71

physiology and metabolism of individuals. Knight (26) established that decomposition can vary from one body to another. Moreover, Salazar-Ortega (27) concluded that notable differences can occur in the decomposition of two cadavers exposed under similar conditions. Contrary to other results (28–30), the duration of a stage in our study could be less, equal, or greater than the following stage within a season (Table 2).

We found more than 54 species of Coleoptera in the carcasses, belonging to 12 families of necrophagous, necrophilous, and omnivorous habits. Availability of these species and families in adult stage through all experiments is given in Tables 3 and 4. Determination of the total mean abundance of each family per carcass per day yielded the following sequence: Histeridae, Dermestidae, Cleridae, Staphylinidae, Nitidulidae, Trogidae, Tenebrionidae, Scarabaeidae, Carabidae, Anthicidae, Melyridae, and Archeocryptidae. The first of them had also the greatest number of species, followed by Scarabaeidae and Tenebrionidae. Seven accidental families were observed as well: Coccinellidae, Chrysomelidae, Carabidae, Curculionidae, Tenebrionidae, Meloidae, and Elateridae, although additional information about these families is not provided here. We recorded families and species with seasonal and annual activity, as other authors observed (7,31,32). This could be a result of environmental factors, which can affect the process of decomposition and succession, as well as of niche segregation. Temporal segregation is a form of coexistence when species appear in different seasons, thus decreasing overlapping. Some species are present only in some seasons, showing marked seasonality (33).

The total amount of beetles found in the experimental pitfall traps was greater or equal to that of the control traps in each season, even when the number of traps was duplicated to ensure that the sampling effort was sufficient. This indicates that the cadavers were an essential factor for insects. Besides the species and tribes found in carcasses, we collected five more species in the experimental traps (Table 4).

The statistical analysis showed that there was no interaction for diversity ( $p > 0.3$ ), which means that decomposition stages behave in a similar way in each season. Figure 1 shows that F + B and winter were the stage and season with less diversity ( $p < 0.05$ ). On the other hand, we found an interaction for abundance ( $p < 0.0001$ ), so in each season, the stages did not behave in the same manner. Figure 2 shows that the pattern of decomposition was mostly similar between seasons except for summer. This pattern involved an increase in abundance from the F + B stage until Advanced Decay. When focusing on the taxocenosis of beetles, we found that the Advanced Decay and Remains were the most abundant ( $p < 0.05$ ); in summer, the Advanced Decay and Active Decay exhibited the greatest number of beetles ( $p < 0.05$ ). The specific diversity exhibited temporal modifications, as ecological successions do (34). Winter was the less diverse season, which could be explained by the low temperatures reported for the period, as was previously

suggested in relation to speed of decomposition. As pointed by Smith (35), the activity of insects decreased or ceased during that season. This could be different in other climatic regions of Argentina. F + B was the less diverse stage, which might be due to the fact that cadaveric decomposition and fauna associated with it can be likened to a heterotrophic succession (36,37).

Of the six families statistically analyzed, five of them exhibited interaction: Dermestidae ( $p < 0.015$ ), Staphylinidae, Histeridae, Cleridae, and Scarabaeidae ( $p < 0.01$ ). The remaining family, Tenebrionidae, did not show differences in any of the variation sources ( $p > 0.3$ ). When association patterns of families with decomposition stages and seasons were analyzed, three main groups of beetles were observed (Fig. 3). Segura et al. (8) studied relation only with decomposition stages and found that all families formed one group. Furthermore, our results showed that Dermestidae predominated in winter throughout the whole process; Staphylinidae showed a high level of association with F + B in spring, summer, and autumn, whereas Histeridae and Cleridae were associated with the subsequent stages during those seasons. Contrary to our findings, Segura et al. (8) observed that all families were associated only with Remains. Furthermore, in our study, Histeridae and Cleridae could be separated into two groups through the cluster results. Segura et al. (8) may have used a statistical methodology that did not allow them to properly distinguish the beetle assemblages. The results reported here are the first to clearly discriminate the assemblages of beetle families with respect to seasons and decomposition stages.

Histeridae was represented by *Phelister* sp., *E. pavidus*, *E. patagonicus*, *E. lacordairei*, and *E. ornatus*. In winter, the family did not show significant variations between the decomposition stages ( $p > 0.05$ ). During spring, clown beetles were observed in greater numbers during Advanced Decay, followed by Remains ( $p < 0.05$ ). In summer, the family was abundant in Active and Advanced Decay ( $p < 0.05$ ). During autumn, there were no significant differences in the number of histerids during the decomposition process ( $p > 0.05$ ). Histeridae was more dominant from Active Decay to Remains during spring and in Active Decay in summer. This family was also recorded in greater abundance during these periods. The dominance of these beetles could be related to a decrease of rove beetles and the low levels of abundance in the other families. Certainly, during the first stages of decomposition, when the dominance of rove beetles was greater, that of histerids was lesser. Moreover, in summer, the presence of clown beetles decreased during Advanced Decay followed by Remains, which coincided with an increase in the proportion of clerids. Although our results are inconclusive due to the experimental design, they may be explained by the feeding habits of clown beetles, which are necrophiles and therefore will compete with Cleridae and Staphylinidae for the same food source (38–41). Larvae of Histeridae were more abundant in Advanced Decay and Remains during autumn and only in the last stage during spring, possibly because they can feed on

TABLE 3—Mean abundance of the species or minimum taxonomic level registered per carcass (c) and day, during each stage of decomposition per season of the year.

Species and tribes	Winter					Spring					Summer					Autumn				
	F	B	AD	ADD	R	F	B	AD	ADD	R	F	B	AD	ADD	R	F	B	AD	ADD	R
Anthicidae sp. <sup>O</sup>				○					○	○										
<i>Archeocrypticus topali</i> <sup>Ne</sup>				○																
<i>Astylus</i> sp. <sup>Ne</sup>				○	○										○					
Harpalini <sup>Ne</sup>			○	○			○													
Cyclosomini, Lebiini, Pterostichini, Bembidiini <sup>Ne</sup>	○	○	○	○	○										⊕					
<i>Necrobia rufipes</i> <sup>O</sup>		⊕	⊕	⊕	⊕			○	●	●			●	●	●		⊕	●	●	●
<i>Dermestes maculatus</i> <sup>N</sup>	●	●	●	●	●			●	●	●			●	●	●		●	●	●	●
<i>Carcinops</i> sp. <sup>Ne</sup>														⊕	○					
<i>Euspilotus</i> sp. <sup>Ne</sup>																				○
<i>Euspilotus</i> (H) <i>caesopygus</i> <sup>Ne</sup>			○				○		○											
<i>Euspilotus</i> (H) <i>connectens</i> <sup>Ne</sup>									○											
<i>Euspilotus</i> (ss) <i>lacordairei</i> <sup>Ne</sup>			○				○	○	○				○	○		⊕	⊕	⊕		○
<i>Euspilotus</i> (H) <i>niger</i> <sup>Ne</sup>									○											
<i>Euspilotus</i> (ss) <i>ornatus</i> <sup>Ne</sup>			⊕		○		⊕	⊕		⊕			○	○	○		⊕	⊕		○
<i>Euspilotus</i> (ss) <i>patagonicus</i> <sup>Ne</sup>			○		○		⊕	○	○	○			●	●	○		⊕	⊕	⊕	○
<i>Euspilotus</i> (H) <i>pavidus</i> <sup>Ne</sup>	○	○	●	⊕	⊕		●	●	●	●			●	●	⊕		○	○	⊕	○
<i>Phelister</i> sp. <sup>Ne</sup>			●	○	○		○	⊕	●	●			●	●	⊕		⊕	○	⊕	⊕
<i>Xerosaprinus</i> (X) <i>diptychus</i> <sup>Ne</sup>										⊕										⊕
Dendrophilinae sp. <sup>Ne</sup>													⊕	⊕						
Histerinae sp. 1 <sup>Ne</sup>																	○	○		○
Histerinae sp. 2 <sup>Ne</sup>																				⊕
<i>Nitidula carnaria</i> <sup>O</sup>			●	●	●				⊕	○			●	●	●				○	
<i>Gondwanocrypticus platensis</i> <sup>Ne</sup>			○		○													○		
<i>Hylitus tentyroides</i> <sup>Ne</sup>	○	○	○	○	○		○	○		○										○
<i>Leptynoderes strangulata</i> <sup>Ne</sup>			○																	
<i>Scotobius casicus</i> <sup>N</sup>			○																	
<i>Scotobius milliaris</i> <sup>N</sup>			○		○		○			○			○	○						○
<i>S. muricatus</i> <sup>N</sup>			⊕		⊕		○			⊕			○	○						○
<i>A. pseudolividus</i> <sup>N</sup>			○		○					○			○	○						○
<i>A. chaconus</i> <sup>Ne</sup>			○																	
<i>Archophileurus fodiens</i> <sup>Ne</sup>										○										
<i>Ataenius platensis</i> <sup>N</sup>			○					○	○	○					○			○		○
<i>Canthon ornatus bipunctatus</i> <sup>N</sup>			○		○		○						⊕		○					
<i>Ontophagus</i> sp. <sup>N</sup>									○	○										
<i>Pseudocanthos</i> sp. <sup>N</sup>										○										
Aleocharinae spp. <sup>Ne</sup>	○	⊕	⊕				⊕	●	●	●			⊕	●	●			●	●	○
<i>Carpelimus</i> spp. <sup>Ne</sup>	⊕	●	●		○		●	●	●	●			○	○	○			●	●	●
<i>Creophilus maxillosus</i> <sup>Ne</sup>	○	○	○						○	○			○	○	●					○
<i>Haematodes bicolor</i> <sup>Ne</sup>																				○
<i>Philonthus flavolimbatus</i> <sup>Ne</sup>	○	○	○				○	●	●	⊕			⊕	○				○	⊕	
<i>Omorgus batesi</i> <sup>N</sup>			○		○			○		○					○					
<i>Polynoncus gemmingeri</i> <sup>N</sup>			○		●			○	⊕	●				⊕	⊕					○

F: Fresh; B: Bloat; AD: Active Decay; ADD: Advanced Decay; R: Remains; N: Necrophages; Ne: Necrophiles; O: Omnivores; White space: 0 individuals/c/day; ○ < 0.33 individuals/c/day; ⊕ < 1 individuals/c/day; 1 < ● < 3.33 individuals/c/day; ● > 3.33 individuals/c/day.

dipteran larvae and other soft-bodied organisms (42,43), which disperse during those stages; moreover, there are larvae of necrophagous beetles that can serve as an alternative food source for Histeridae. Our results in this matter are very relevant, given that only one Histeridae larva had ever been reported for Argentina thus far (44).

Dermestidae was represented only by *D. maculatus*. During winter and spring, this species was found in greater numbers in Advanced Decay and Remains ( $p < 0.05$ ). In summer, skin beetles were more abundant in Active and Advanced Decay ( $p < 0.05$ ). In contrast, during autumn, there were no significant differences in the number of dermestids during the decomposition process ( $p > 0.05$ ). Although skin beetles were present

throughout the year, their abundance and dominance were greater in winter through the whole process and increased as decomposition progressed to the last stages. A possible explanation is that these beetles prefer a narrow niche to reduce competition with dipteran activity (45). The strong association of skin beetles with the coldest season could be related to the long time that the decomposition process took, as well as to a lesser amount of dipteran larvae, which could lead to a long-term availability of food. Catts and Haskell (46) inferred that a long decomposition process could lead to a greater presence of Dermestidae in a body. Other authors have also indicated that a high relative humidity and a short decomposition time could avoid the presence of a dry stage and thus reduce the presence of skin

TABLE 4—Mean abundance of the species or minimum taxonomic level captured in traps (st) per day, during each decomposition stage per season of the year

Species and tribes	Winter					Spring					Summer					Autumn				
	F	B	AD	ADD	R	F	B	AD	ADD	R	F	B	AD	ADD	R	F	B	AD	ADD	R
Anthicidae sp. <sup>O</sup>		○	○	●	●			●	●	●			●	●	●		●	○	●	○
<i>Archeocrypticus topali</i> <sup>Ne</sup>				○				○	○	○										
<i>Astylus</i> sp. <sup>Ne</sup>				○	○															
Harpalini <sup>Ne</sup>	○			●	○					●	●	●	○							
Cyclosomini, Lebiini, Pterostichini, Bembidiini <sup>Ne</sup>	●	●	●	●	●	●	●	●	●	●					○		○		○	○
<i>Necrobia rufipes</i> <sup>O</sup>				○	○				○	○				●	○				●	●
<i>Dermestes maculatus</i> <sup>N</sup>			●	●	●	○		●	○	○			●	●	○		○	○	○	○
<i>Carcinops</i> sp. <sup>Ne</sup>										○				●	○					
<i>Euspilotus</i> sp. <sup>Ne</sup>									●											
<i>Euspilotus (H) caesopygus</i> <sup>Ne</sup>				○																
<i>Euspilotus (H) connectens</i> <sup>Ne</sup>								●	●	○										
<i>Euspilotus (ss) lacordairei</i> <sup>Ne</sup>				○	○			●	●	○			●	●	○	●	●	○		
<i>Euspilotus (H) niger</i> <sup>Ne</sup>													●							
<i>Euspilotus (ss) ornatus</i> <sup>Ne</sup>			○	●	○	●	●	●	●	●			●	●	○	○	○	○	○	○
<i>Euspilotus parenthesis</i> <sup>Ne</sup>									○											
<i>Euspilotus (ss) patagonicus</i> <sup>Ne</sup>				○				○	●	○			●	●	○					○
<i>Euspilotus (H) pavidus</i> <sup>Ne</sup>				○	○			●	●	●			●	●	●					○
<i>Phelister</i> sp. <sup>Ne</sup>				●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○
<i>Xerosaprinus (X) diptychus</i> <sup>Ne</sup>									○											
Dendrophilinae sp. <sup>Ne</sup>					○								●	●						
Histerinae sp. 1 <sup>Ne</sup>																				○
Histerinae sp. 2 <sup>Ne</sup>										○										○
<i>Nitidula carnaria</i> <sup>O</sup>										○				●	○					○
<i>Blapstinus punctulatus</i> <sup>Ne</sup>				●	●	○	○	●	○	●	●	●	●	○						○
<i>Gondwanocrypticus platensis</i> <sup>Ne</sup>				●	●	●	●	●	●	●	●	●	●	○						○
<i>Hylitus tentyroides</i> <sup>Ne</sup>	●	●	○	●	●			●		○	●	●	○							○
<i>Leptynoderes strangulata</i> <sup>Ne</sup>				○	●				○							○	○	○		
<i>Scotobius casicus</i> <sup>N</sup>				●	●				○	○										
<i>Scotobius milliaris</i> <sup>N</sup>				●	●			○	●	○	○	○	○	○		○	○			
<i>Scotobius muricatus</i> <sup>N</sup>	○			○	○	○			○	○	○	○	○		○					
<i>Trichoton roigi</i> <sup>Ne</sup>				○	○					○										
<i>Aphodius militaris</i> <sup>N</sup>				○	○			○	●	○	○	○	○	○	○	○	○	○	○	○
<i>Aphodius pseudolividus</i> <sup>N</sup>				○	○			○	●	○	○	○	○	○	○	○	○	○	○	○
<i>Archophileurus chaconus</i> <sup>Ne</sup>				○									○	○	○					○
<i>Archophileurus fodiens</i> <sup>Ne</sup>				○	○								○	○	○					○
<i>Ataenius platensis</i> <sup>N</sup>				○	○	○	○	○	○	○			○	○	○					○
<i>Canthon ornatus bipunctatus</i> <sup>N</sup>				○	○					○			○	○	○					○
<i>Degallieridium</i> sp. <sup>N</sup>										○										
<i>Pseudocanthon</i> sp. <sup>N</sup>				○	○					○			○	○	○					
Aleocharinae spp. <sup>Ne</sup>		○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
<i>Carpelimus</i> spp. <sup>Ne</sup>	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
<i>Creophilus maxillosus</i> <sup>Ne</sup>									○	○					○					○
<i>Haematodes</i> sp. <sup>Ne</sup>								○												
<i>Haematodes bicolor</i> <sup>Ne</sup>																				○
<i>Philonthus flavolimbatus</i> <sup>Ne</sup>						○	○	●	●	○										
<i>Omorgus batesi</i> <sup>N</sup>				○	○			○		○					○					
<i>Polynoncus gemmingeri</i> <sup>N</sup>					○				○	○	○	○			○					

F: Fresh; B: Bloat; AD: Active Decay; ADD: Advanced Decay; R: Remains; N: Necrophages; Ne: Necrophiles; O: Omnivores; White space: 0 individuals/st/day; ○ < 0.33 individuals/st/day; ● < 0.33 < 1 individuals/st/day; ○ < 1 < 3.33 individuals/st/day; ● > 3.33 individuals/st/day.

beetles in corpses (47). Moreover, the low number and the presence of other beetles such as Cleridae and Histeridae could probably contribute to the greater dominance of skin beetles. We

also found larvae that were predominant in all seasons, mainly in the last stages, which could be related to the strong preference of larvae for dry substrate, bone, and cartilage (45,48).

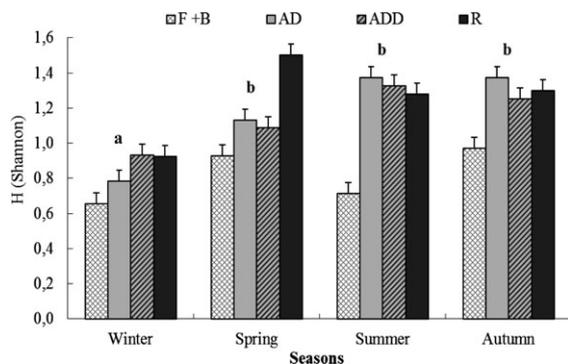


FIG. 1—Specific diversity of beetles observed in cadavers per decomposition stages during each season (Mean ± SE). Medias that shared the same letter did not differ significantly (DMS,  $p > 0.05$ ). F + B: Fresh stage + Bloated stage; AD: Active Decay; ADD: Advanced Decay; R: Remains.

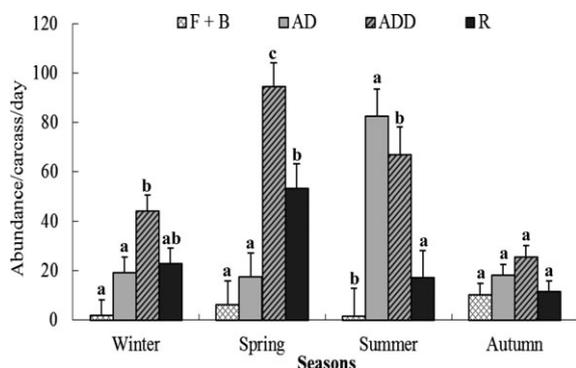


FIG. 2—Mean total abundance (±SE) of adult beetles found in cadavers per decomposition stages and seasons. Medias that shared the same letter did not differ significantly (DMS,  $p > 0.05$ ). F + B: Fresh stage + Bloated stage; AD: Active Decay; ADD: Advanced Decay; R: Remains.

Nonetheless, it was during the coldest season when the largest capture was obtained. This could be explained by the dominance that adults exhibited during that season. Furthermore, in summer and autumn, we observed larvae of fourth, fifth, and sixth instars during Bloated and Active Decay stages, which could be attributed to the presence of a dead animal in the proximity of the cadaver being used, meaning that larvae could have fed from another dead animal and then gone to the experimental cadaver to complete their development. In this way, may be those larvae could also be remnant from the previous experiment performed in the area. This could be similar to postdispersal movement of dipteran larvae, which search for a place to pupate or another source of food if their resources of fat are insufficient to pupate (49). This could lead to errors in the estimation of PMI, because the time of death indicated by the age of larvae would be earlier than the actual time of death.

Cleridae was represented only by *N. rufipes*. In winter, clerids did not show significant variations between decomposition stages ( $p < 0.05$ ). During spring, they were abundant in Advanced Decay and in Remains ( $p < 0.05$ ). In summer, the greatest number of these beetles was observed during Advanced Decay, followed by Active Decay ( $p < 0.05$ ). During autumn, they were more abundant in Advanced Decay ( $p < 0.05$ ). Although clerids were found throughout the year, they were

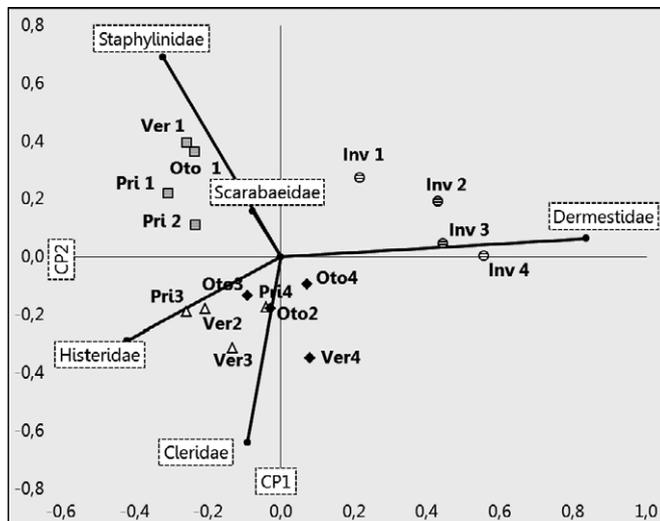


FIG. 3—Biplot with variables represented from an auto-vector matrix (vectors) and rows in their norm (points) (76% of composition). A: autumn; Sp: spring; Su: summer; W: winter. 1: F + B (Fresh stage + Bloated stage); 2: Active Decay; 3: Advanced Decay; 4: Remains. Different symbols respond to each group that resulted from the cluster.

more abundant in summer during Active Decay and Advanced Decay, and their dominance was greater during Advanced Decay and Remains, whereas during autumn, these beetles were dominant from Active Decay to Remains. Our observations indicate that these beetles dominated when the relative frequency of rove and clown beetles decreased. Clerids are mostly predators but there are exceptions, indicating that they can be omnivorous, too, predated on dipteran and coleopteran larvae, and eating animal or human tissues (50–52). A larva was observed in Advanced Decay during autumn. It is likely that more individuals were present but could not be seen because pupal chambers are difficult to detect. However, Battán-Horenstein and Linhares (17) collected many of them in the later stages of decomposition, which could be a result of the methodology (a Schoenly trap) they employed.

Staphylinidae was represented by *Carpelimus* spp. and *Aleocharinae* spp., followed by *P. flavolimbatus* and *C. maxillosus*. During winter, rove beetles were more abundant in Active Decay than in Remains ( $p < 0.05$ ). In spring, these beetles were in greatest number during Active Decay and Advanced Decay ( $p < 0.05$ ). During summer, they were more abundant in Active Decay ( $p < 0.05$ ). In autumn, the greatest number of beetles was recorded during F + B and Advanced Decay ( $p < 0.05$ ). Rove beetles were dominant during the first stages of decomposition, decreasing their dominance as the process advanced, which was also coincident with an increase in abundance of other families such as Dermestidae during winter, Histeridae during spring, and Cleridae during summer and autumn. These results could be a consequence of the predatory role that rove beetles have. They can feed on larvae of Diptera and other insects (27,35,47), and some are parasites of puparia of dipterans (53). Larvae were found in low number during winter, spring, and autumn in a different stage during each season. In general, larvae feed on eggs and larvae of Diptera and other soft-bodied organisms (42,43), sharing their habitat with adults.

*Nitidula carnaria*, a species first mentioned in South America in Zanetti et al. (54), was the only member of Nitidulidae we

recorded. Nitidulidae were more abundant in summer, followed by winter, and throughout the experiments, they were recovered from Active Decay to Remains. Nitidulidae can feed from fluids and exudates of decomposing organic matter, including plant or animal tissues (55–57). Some nitidulid species are omnivorous (35,58). According to several authors, these beetles arrive during the later stages of decomposition, particularly when corpses are dry, and they coexist with dermestids (59–61). Food is a prerequisite for the production of pheromones (62,63) which is important for the aggregation and reproduction of these beetles. In fact, we found larvae in a cadaver during Advanced Decay in winter, in an area of rotten tissue with fat and moist. In another study performed in Chile, larvae were also observed under such conditions (64). Byrd and Castner (65) suggested that nitidulids prefer wet environments.

Trogidae was represented by *P. gemmingeri* and *O. batesi*. The first was the most abundant and frequent, particularly in the last stages of decomposition. This could be due to their feeding habits, because keratin is a main component in their diet, and so they can be found among feathers, fur, skin, feces, and leather of bodies, and also skeletons with or without little tissue (66,67); another relevant factor is their ability to reproduce in carrion. This family has been scarcely reported in Argentina in forensic entomology studies (17,68–70).

Tenebrionidae did not exhibit differences in any of the variation sources. They were observed in all seasons, from the beginning to the end of the decomposition process. Their trophic roles may be the reason for this result, because some of them feed on dead animal matter (71). In this work, the more representative species were *H. tentyroides*, *S. millaris*, *G. platensis*, and *S. muricatus*. This family was also present as larvae, being less abundant during winter.

Scarabaeidae was represented by *C. ornatus bipunctatus* and *Pseudocanthon* sp. in corpses, while *Aphodius pseudolividus*, *A. militaris*, and *Ataenius platensis* were notorious in traps. This is the first report of the family in Argentina in forensic entomology studies. Although, Damborsky et al. (72) used pitfall traps baited with carrion to attract Scarabaeidae, the purpose of the research and the type of carrion were different. Moreover, finding scarab beetles in a decomposition process involves more than one methodology (attracting with baited traps) and the information which can be obtained is varied and can confirm the character (cadaveric) of these beetles because, for example, not only can be known their feeding sources but also if they reproduce in that habitat. During winter, scarab beetles did not show significant variations between the decomposition stages ( $p > 0.05$ ). In spring, they predominated in the last stage ( $p < 0.05$ ). During summer, scarab beetles were more abundant during F + B ( $p < 0.05$ ). In autumn, the number of these beetles did not show significant differences during the process ( $p > 0.05$ ). Also, Scarabaeidae dominated in F + B during the hottest season. This could be related to the presence of *C. ornatus bipunctatus*, a species registered removing cadaveric tissue and building balls with it, which they then moved. Indeed, Ururahy-Rodrigues et al. (73) reported necrophagous specimens of other species, which is also a member of the Scarabaeidae family, colonizing a carcass from the first day in the Adolpho Ducke Forest Reserve in Manaus, Brazil. The species in the genus *Ataenius* are basically saprophagous (74). The presence of *A. chacoensis* and *A. fodiens* in corpses may have occurred because adults of the Scarabaeid tribe Phileurini (Dynastinae) are predators of larvae and adult beetles, among other insects. In this study, larvae of scarab beetles were absent in autumn. The great-

est number of individuals was observed during summer in Remains, as well as in the other seasons. This could be related to the fact that larvae feed on carrion and dry skin (71). This is the first record of scarab beetle larvae in carcasses in Argentina.

Carabidae was mostly represented by *T. chaldeus* and *P. egenus*. During winter, this family was found from Bloated stage until Remains, and in the other seasons, specimens were collected in one or both of the following stages: F + B, Advanced Decay, or Remains. Ground beetles were seen around eggs, larvae, pupae, and adults of other insects, so they were considered as necrophiles. Scampini et al. (75) suggested that because of the constant presence and abundance of some species, they should be considered as part of the cadaveric fauna, particularly as predators of larvae of other groups of insects such as Diptera. In our study, larvae of Carabidae were present in winter and autumn. Larvae generally hide during the day and feed during the night; most of them feed on dry or dead animals, and other live insects such as larvae of Diptera, beetles, among others (71).

Anthicidae was represented by a species which could not be identified because of the lack of taxonomical keys, as reported in another study (17). They were captured all year, mainly during Advanced Decay and Remains. Their presence may have been recorded in the coldest season because that assay was prolonged into spring, because the greatest abundance of beetles was captured in spring months.

Archeocrypticidae was represented by *A. topali* found during winter and spring. This is the first time this species is reported for Buenos Aires Province.

Melyridae was represented by *Astylus* sp. In cadavers, beetles were collected in winter during the last stages and in summer during Remains. Their presence could be related to the fact that most adults and larvae are predators (76). Practically, no reports of this family have been made in other carrion studies.

A more detailed analysis of the taxocenosis of beetles revealed the following succession in cadavers. During winter, Dermestidae coexisted with rove beetles in the first stages, and rove beetles were then replaced by dermestids as the decomposition process progressed. Dermestids also played an important role in Remains during the other seasons. During spring, rove beetles were in major presence in F + B followed by clown beetles. Inversely, clown beetles dominated in Active Decay, followed by rove beetles, which continued being replaced by clown beetles in the following stages. In summer, F + B was dominated by Staphylinidae and Scarabaeidae, but they were replaced by Histeridae during Active Decay, as well as by Cleridae. Furthermore, Cleridae replaced clown beetles in Advanced Decay and Remains. During autumn, rove beetles represented a large proportion of composition in F + B, but in the three subsequent stages, Cleridae became dominants.

## Conclusions

All the results reported in this work represent new information that can be applied in forensic cases and underline the importance of performing studies in different geographic areas to obtain data on cadaveric fauna.

New records of families and species of forensic interest for the province of Buenos Aires, Argentina and South America are included.

Families and species of cadaveric importance exhibited annual and seasonal activity. Seasonal differences in the presence and activity of species can be of relevance in PMI estimation, particularly in the region where our study was conducted, determining

in which season death happened; this is especially relevant when a long time has passed since death.

The specific diversity, total average abundance, and average abundance of beetle families can be affected by seasons and the stage of decomposition at which the corpse is. Knowing how these variables can change in the different seasons and stages of decomposition assist in interpreting insect succession.

Because Histeridae was the most diverse and abundant of the families, as well as the ecological role this family has in corpses, it is necessary to remark their forensic potential and to study their life cycles (mostly unknown) for forensic purposes.

The taxonomic composition of beetles also changed with the stages of decomposition and seasons. This allowed us to establish the times of colonization, which is of great use to accurately estimate the time of death during early and later stages of decomposition. Three assemblages of beetles could be distinguished: one from winter (Dermestidae), one with rove beetles in almost all the year in F + B, and one with Histeridae and Cleridae in the subsequent stages. Furthermore, Dermestidae was important in later stages during the other seasons. Through these results, we are able to clearly discriminate for the first time the assemblages of beetle families in a semirural area of the temperate region of Argentina.

We found larvae of certain families; in general, Dermestidae was the most abundant family in all seasons. These results are of great relevance because they provide a record of the families which reproduce in a cadaver, therefore allowing taxonomical studies of larvae and of the life cycles of species at different temperatures. Estimations of the PMI can thus be made, especially when large periods of time have passed since the beginning of decomposition. Moreover, the fact that larvae were found in pit-fall traps and 4th, 5th, and 6th instar larvae were observed in corpses during the Bloated and Active Decay stages in summer and autumn suggests that these stages have a great ability to move in search for food or protection to complete their development. This behavior resembles that of Diptera, which should be considered when collecting those immature stages in the proximity of a cadaver and estimating PMI in advanced stages of decomposition, as well as to avoid errors in the estimation of PMI, because the age of larvae might overestimate the time elapsed since death.

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Additional information and reprint requests:

Néstor D. Centeno, Ph.D.

Laboratorio de Entomología Aplicada y Forense

Departamento de Ciencia y Tecnología

Universidad Nacional de Quilmes

Sáenz Peña 352

Bernal 1876

Provincia de Buenos Aires

Argentina.

E-mail: ncenteno@unq.edu.ar