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A Statistical Analysis of Successional Patterns in Carrion-Arthropod Assemblages: Implications for Forensic Entomology and Determination of the Postmortem Interval

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ABSTRACT: A set of statistical protocols is proposed for analyzing carrion-arthropod succession in forensic entomology investigations. A total of 23 carrion-arthropod data sets from temperate, tropical, desert, and coastal environments were assembled in a standard format and analyzed using randomization tests and methods derived from quantitative community ecology. The data were analyzed in three ways.

First, patterns of arthropod visitation on nonhuman carcasses were analyzed in each of the 23 cases. Analysis revealed two groups of taxa: those that persist on the carcass over a single time interval (= nonreoccurring taxa, 80% of the taxa) and those that appear, leave, and reappear over time on the carcass (= reoccurring taxa, 20%). Reoccurring taxa, which can confound estimation of the postmortem interval (PMI), were found in 6 classes, 12 orders, and 29 taxonomic families of arthropods, including some forensically important taxa (for example, calliphorids, sarcophagids, histerids). The recognition that reoccurring taxa exist and that they are found in forensically important groups is an early step toward factoring in their potential importance in future entomological investigations.

Second, temporal changes in the taxonomic composition of the carrion-arthropod community were studied by quantifying the degree of taxonomic similarity between pairwise combinations of time-specific samples of the succession. In 13 of the 18 illustrated cases, the midsuccessional samples, owing to their higher species richness, were taxonomically more similar to all other pairwise samples, on the average, than early and late successional samples which were poorer in species. Variability in taxonomic composition is the norm for most periods of the succession; however, in 17 of the 23 cases, some successional periods (particularly endpoint samples) revealed no changes in arthropod species composition (= matching sample-pairs). When applied to medicolegal cases, it is suggested that data sets with large fractions of matching sample-pairs should produce wider-ranging PMI estimates, on the average, than data sets with smaller fractions of matching sample-pairs.

Third, Monte Carlo simulation was applied to each of the 23 assemblages to test specific hypotheses about community-wide patterns of arthropod visitation times on nonhuman carcasses. Simulation results revealed that arthropod residence times in the majority of cases (13 or 56%) followed a "clumped" succession model, whereas, the remaining 10 cases (44%) showed a more "uniform" spacing pattern of residence times on carcasses. Comparison of species accumulation curves for observed and simulated data further revealed that among the 13 "clumped" cases, most (9 or 69%) followed a "clumped, early" model (rather than "clumped, midterm" or "clumped, late" models). These nine cases were shown to be con-

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sistent with evolutionary biology considerations. Possible uses of these methods to detect (or validate claims of) between-site, between-treatment, or between-taxon differences in carcass decay rates are revealed.

The proposed methods and findings may prove useful to forensic entomologists in hypothesis testing, field studies of carrion-arthropod succession, and PMI estimation of human remains in medicolegal cases.

KEYWORDS: pathology and biology, entomology, carrion-arthropod succession, statistical protocols, postmortem interval, carrion insects, decay rates, sampled randomization tests, Monte Carlo simulation, statistical baselines, community overlap, similarity

Forensic entomologists apply accumulated knowledge of developmental and successional (= species replacement) timetables of carrion-frequenting arthropods (mostly flies) to aid medicolegal investigators in estimating the postmortem interval (PMI) in human remains cases. Since the first recorded use of entomology in a criminal case in thirteenth-century China [1], work in forensic entomology has been episodic [2,3], but recent years have seen a resurgence in the discipline [4–8]. Current knowledge of carrion-arthropod succession, however, is still largely descriptive or anecdotal; thus, the development of statistical protocols in forensic entomology seems overdue. Just as beginning medical students require knowledge of physiologic baselines in healthy individuals to judge abnormal or pathological states in the sick, forensic entomologists require statistical baselines on successional (and developmental) patterns of carrion-arthropod faunas to evaluate human-remains cases.

In a previous study, Schoenly and Reid [9] applied univariate and multivariate statistics to analyze successional trends in eleven carrion-arthropod communities. This study, which explored basic (ecologic) rather than applied (forensic) properties of carrion-arthropod succession, revealed several between-study similarities of day-to-day changes in total species, new arrivals and local extinctions on nonhuman carcasses. Qualitatively, the pattern of species-specific daily changes followed a relatively predictable sequence: (1) rapid invasion by (mostly) ants and dipterans within the first 16 days of observation; (2) a peak in species richness (days 7 to 26) when the carcass was presumably most attractive to sapsaprophagous arthropods and their predators and parasitoids; (3) gradual decline in species richness as more emigrations of early successional species occurred; and (4) in the final days of carcass observation (up to and including the skeletal remains period), a small “endpoint” assemblage prevailed, typically comprised of trogid beetles, mites, dermestid beetles, tineid moths, and other taxa. The statistical methods used in this study, aside from aiding the discovery of these successional patterns, provided limited application to forensic entomology.

Consequently, this is the first study (as far as I am aware) to propose statistical protocols in forensic entomology. Here, I use 23 carrion-arthropod assemblages, sampled randomization tests (Monte Carlo simulation) and methods derived from quantitative community ecology to explore general successional trends—applicable to forensic entomology—to ask: (1) Do carrion-arthropod taxa show predictable patterns of carcass visitation? (2) How does the taxonomic composition of the carrion-arthropod community change over successional time? and (3) Do carrion-arthropod assemblages show random, clumped, or uniform spacing of their taxa? The resulting analyses produced a set of statistical baselines that may prove useful to forensic entomologists in hypothesis testing, field studies of carrion-arthropod succession, and PMI estimation of the deceased.

Data Sources and Standardization

Twenty-three data sets from 14 published (and two unpublished) sources were included in this statistical study (Table 1). Collectively, the 16 carrion ecology and forensic en-

tomology reports cover most latitudes: seven are from temperate climates [10–16], five are from the tropics [17–21], and three are from desert sites [22–24]; the remaining study was located along a stretch of New England coastline [25].

In each of the 16 studies, most carrion-frequenting taxa were identified to species or genus, whenever possible; hence, taxonomic resolution within these reports is generally uniform across all animal groups. In addition, some of the studies also reported times when egg, larvae, pupae and/or adult stages of individual dipteran and coleopteran species were present. Such reporting was more prevalent in forensic entomology reports [15,18–20,25] than carrion ecology studies [10–14,16,17,21–24]. Lumping biological species into higher taxonomic groups was unavoidable for some arthropods (for example, staphylinid beetles, collembolans, dermapterans, isopteran) and reflected either poorly known taxonomy, final determinations by consulting taxonomists/systematists, or a difficulty of the original author(s) to distinguish morphologically similar taxa in the field [9]. Aside from these differences, however, the form of data reporting in these 16 carrion ecology and forensic entomology reports was similar in most respects.

As a reflection of different authors, locations, and types of nonhuman carcasses used, the 23 data sets are nevertheless heterogeneous in several respects. For example, the total length of the observation period varied from six consecutive days (for toad carcasses) in a Costa Rican tropical forest (Guanacaste site, Ref 17) to 220 nonconsecutive days (for guinea pig carcasses) in an Australian chaparral woodland (Ref 11). Between-study variation in the number of samples collected by the authors ranged from six samples (Ref 17) to 39 (Refs 15,22,23) with a mean of 20 samples taken during the observation period (Table 1); the mean time interval between consecutive samples ranged from one day (11 cases) to 10.4 days in Bornemissza's guinea pig study (grand mean: 2.1 days; Table 1). Also, the authors' choice of carcasses were from whole (mostly previously frozen) animals and they spanned four vertebrate classes (Amphibia, Reptilia, Mammalia, Aves) and a wide biomass range (27 g to 65 kg). Other biotic and abiotic factors, such as air, soil and carcass temperatures and degrees of vertebrate scavenger participation, if these variables were consistently recorded in the 14 published reports, would likely show appreciable between-study variation. Thus, early recognition of these differences made adoption of a data standardization procedure a necessity before analysis could begin.

Authors of carrion studies typically combine data from replicate carcasses into a single succession diagram or table (Fig. 1A). This has the effect of producing a 'cumulative' portrait of carrion-arthropod succession for a given location and time of year. From each succession diagram or table reported by an author, I constructed an occurrence matrix, containing N columns of time-specific samples and T rows of carrion-arthropod taxa (Fig. 1B). In all but five reports [10,16,17,24,25], taxa were recorded as simply present or absent. To facilitate cross-system study, I adopted this qualitative (binary) mode of reporting for all 23 assemblages. Thus, when taxon A was found in sample 1 (or day 1 in many cases) a '1' was inserted in row A and column 1 of the occurrence matrix; otherwise there was a '0'. The number of nonzero entries in a given column indicated the taxonomic richness of that sample, whereas, the number of nonzero entries in a given row indicated the number of occurrences or the 'residence time' (in some cases) of that taxon on the carcass (Fig. 1B). Converting published listings into binary matrices also provided a convenient machine-readable format of data storage and retrieval for other types of successional analyses, such as PMI estimation [26].

Do Carrion-Arthropod Taxa Exhibit Predictable Patterns of Carcass Visitation?

This section focuses on patterns of arthropod visitation on carcasses. One visitation pattern investigated here involves two groups of taxa: taxa that appear and leave over a single time interval (hereafter called "nonreoccurring taxa"); and taxa that appear, leave,

TABLE 1—Characteristics and summary statistics of 23 carrion-arthropod assemblages.

Type of carcass(es) used and location of study (grouped by environment)	No. of taxa (T) ^a	No. of time-specific samples (N)	Average between-sample interval (in days) ^b	% of matching sample-pairs (%MS-P)	Number of intervals taxon was observed ^c					Grand mean of paired-sample similarities (S_{mean})	Observed overlap (O_{obs})	Ref(s)
					1	2	3	4	5			
					(% of taxa)							
Rabbits, Juniper Hall Field, Centre, England	21	14	1	1.1	38	43	19	0	0	0.299	460	10
Guinea pigs, King's Park, W. Australia	47	26	10.4	4.6	78	22	0	0	0	0.565	9323	11
Dogs, Knoxville, Tennessee	35	21	2.3	1.4	100	0	0	0	0	0.397	4408	12
Bank voles, Ojców National Park, Poland (summer, underground)	29	30	1	1.1	86	14	0	0	0	0.390	2203	13
Bank voles, Ojców National Park, Poland (summer, aboveground)	31	28	1	3.4	61	39	0	0	0	0.218	1929	13
Various mammals, Carle Woods, Illinois	21	13	3.7	3.8	86	14	0	0	0	0.597	1618	14
Red fox, Great Britain	63	39	2.3	0.5	95	5	0	0	0	0.275	3235	15
Turtles, Seekonk, Massachusetts	12	16	1	0.8	42	25	8	17	8	0.430	408	16
Toads, Rincón de Osa, Costa Rica	10	9	1	2.8	60	40	0	0	0	0.318	115	17
Toads, Guanacaste, Costa Rica	9	6	1	0	100	0	0	0	0	0.406	58	17
Lizards, Rincón de Osa, Costa Rica	18	10	1	0	50	33	17	0	0	0.342	576	17
Lizards, Guanacaste, Costa Rica	13	7	1	4.8	100	0	0	0	0	0.564	248	17

Dog, Central Valley, Costa Rica	12	37	2.5	11.0	92	8	0	0	0	0.407	815	18
Cats, Manoa Valley, O'ahu, Hawaii	39	26	2.6	0.9	90	10	0	0	0	0.478	4716	19,20
Cats, Diamond Head Crater, O'ahu, Hawaii	38	26	3.0	0	95	5	0	0	0	0.395	2542	19,20
Impala, Kruger National Park, South Africa (winter succession)	16	23	1	12.6	100	0	0	0	0	0.456	677	21
Rabbits, White Sands National Monument, New Mexico	24	39	2.0	3.8	88	12	0	0	0	0.631	3395	22,23
Rabbits, Aden Crater, New Mexico	20	11	1	18.2	100	0	0	0	0	0.808	838	22,23
Rabbits, Hueco Mountains, Texas	46	26	1	0.9	93	7	0	0	0	0.471	4022	22,23
Jackrabbits, Franklin Mountains, Texas	12	7	2	0	92	8	0	0	0	0.614	226	24
Cottontail rabbits, Franklin Mountains, Texas	12	6	2	0	58	42	0	0	0	0.595	157	24
Gulls, coastal thickets, Isles of Shoals, New Hampshire—Maine	20	19	1.9	0	65	20	5	10	0	0.463	732	25
Gulls, cobble beaches, Isles of Shoales, New Hampshire—Maine	19	17	1.9	2.2	79	21	0	0	0	0.379	362	25
Means:	25	20	2.1	3.2	80	16	2	>1	<1	0.456	1872	

^aDerived from listings in succession diagrams and/or tables.

^bWhen time-specific samples were reported at fixed intervals, the average interval is reported without a decimal point. When time-specific samples were reported at irregular intervals, the average interval is reported with a decimal point.

^cThe length of a taxon's interval of occurrence can vary from a single sample to *N*.

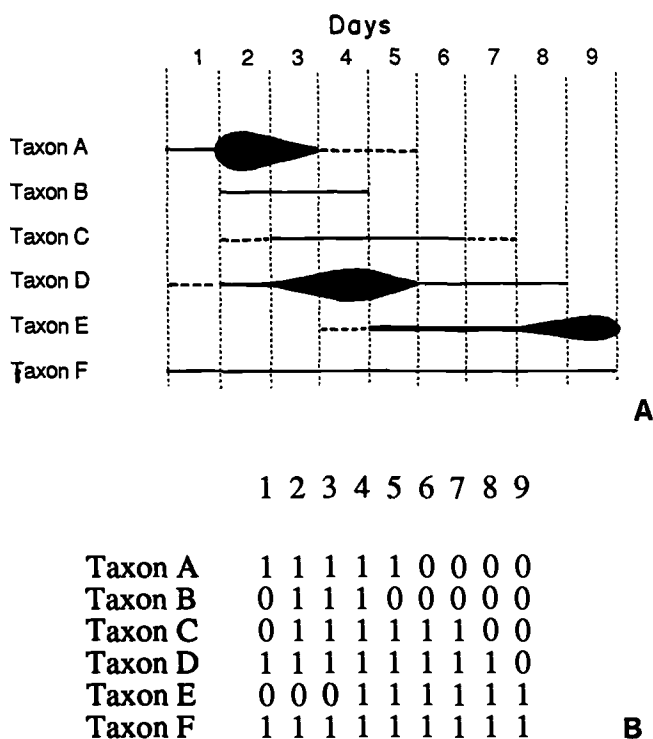


FIG. 1—A, A hypothetical diagram of arthropod succession. A horizontal line of varying thickness denotes different-sized populations of a given taxon for various times in the succession; dashed lines denote single individuals. This graphical format accords with the practice of some earlier investigators. B. Corresponding occurrence matrix. The binary format (1 = taxon presence, 0 = taxon absence) reflected the data standardization procedure adopted in this study.

and reappear on the carcass (hereafter called “reoccurring taxa”). Unlike nonreoccurring taxa, reoccurring taxa can complicate the PMI estimation procedure in death scene cases [26] if they come from forensically important groups (Table 2). For example, if known successional records for reoccurring Taxon A list its presence on days 1 to 3, its absence on days 4 to 7, and its reoccurrence on days 8 to 10, but a subsequent death scene case finds this taxon *present* on a body determined to be 4 to 7 days old (from eyewitness testimony, for example), then the entomologist must decide between including or excluding Taxon A in the estimation procedure. In accord with at least one practitioner [27], one solution entails *using* species determinations from previously verified death cases in the same locality to supplement carrion-based successional records, thus yielding an expanded period of occurrence for a given taxon in a given locality (days 1 to 10 for Taxon A using the above example). Subsequent field experiments and death scene cases could provide additional opportunities for validating successional data in other medicolegal cases. Given the potential importance of reoccurring taxa in forensic cases, this section focuses on their incidence, taxonomic identity, and geographical occurrence.

Methods

For each of the 23 data sets, carrion-arthropod taxa were sorted into reoccurring and nonreoccurring categories. For reoccurring taxa, the statistic of interest here is the interval

TABLE 2—*Reoccurring carrion-arthropod taxa.*

Arthropod Taxon (A = adults, I = immatures)	No. of cases	No. absences between consecutive occurrences ^a	Ref(s)
Class Arachnida			
*Order Acari (A)	3	1,5,7	13,19,20,25
Order Araneae (A)	7	1(×3),2,3,9,10	11,22–25
Order Solpugida (A)	2	1(×2)	24
Class Malacostraca			
Order Isopoda (A)	1	11	11
Class Chilopoda (A)	2	10,19	11
Class Diplopoda (A)	1	5	19,20
Class Symphyla (A)	1	10	11
Class Insecta			
Order Protura (A)	1	10	11
Order Collembola (A)	5	5,7(×2),11,21	13,19,20
Order Orthoptera (A)	2	1,2	17
Order Hemiptera (A)	1	18	11
Order Homoptera (A)	1	16	11
Order Coleoptera			
Family Carabidae (A)	4	1(×2),2,3	10,25
Family Catopidae (A)	4	9(×2),10(×2)	13
Family Corynetidae (A)	1	1	25
*Family Dermestidae (I)	1	1	25
*Family Histeridae (A)	8	1(×6),2(×2)	10,16,17,22,23,25
Family Hydrophilidae (A)	1	1	14
Family Nitidulidae (A)	2	1(×2)	24
Family Scarabaeidae (A)	2	1(×2)	17,24
*Family Silphidae (A)	4	1(×2),2,4	10,16
*Family Staphylinidae (A)	12	1(×6),4,5,9,10,13,28	10,13,15,16
Family Trogidae (A)	1	1	24
unspecified (A)	1	12	11
Order Diptera			
*Family Calliphoridae (A)	4	1(×2),2,3	10,16,18
*Family Drosophilidae (A)	1	1	17
Family Dryomyzidae (A)	1	27	15
Family Heleomyzidae (A)	1	8	13
Family Micropezidae (A)	1	1	17
*Family Muscidae (A,I)	5	1(×2),12,13,14	10,13,17,19,20
Family Otitidae (A)	3	1(×2),7	17,22,23
*Family Phoridae (A)	4	1(×2),2,13	13,14,17
*Family Piophilidae (A)	3	1(×2),2	25
*Family Sarcophagidae (A,I)	7	1(×3),2(×3),4	10,16,19,20,25
*Family Sepsidae (A)	2	1(×2)	16
*Family Sphaeroceridae (A)	2	1,2	17
*Family Syrphidae (A,I)	1	3	16
unspecified (A,I)	5	1(×3),9,18	10,11,13,24
Order Hymenoptera			
Family Andrenidae (A)	1	2	22,23
Family Braconidae (A)	2	1(×2)	10,22,23
Family Cynipidae (A)	1	2	10
Family Formicidae (A)	1	1	14
Family Halictidae (A)	1	2	22,23
unspecified	1	18	11
Total	115		

^aThe number of samples counted between the end of one occurrence interval and the start of the next occurrence interval for a given taxon.

*Forensically important or useful taxa (from taxonomic lists and case studies reported in Refs 6,7).

(number of samples) in which a given taxon is reported absent between consecutive periods of occurrence. By definition, if a reoccurring taxon occurs in a first sample, is absent from a second, and reoccurs in a third, its absence in one sample and its presence for two single-sample intervals would be recorded. For each reoccurring taxon, its period(s) of 'absenteeism,' its taxonomic affiliation and its geographical source were identified.

Results and Discussion

In five of the 23 cases listed in Table 1, all carrion taxa were present for a single interval (Refs 12,17[2 cases],21,23) and in the remaining 18 cases, most taxa were present for a single interval (mean: 80%). In the guinea pig study of Bornemissza [11], for example, 78% of the 47 taxa observed appeared only for a single interval (= nonreoccurring taxa), never reoccurring after once going locally extinct; the remaining 22% of taxa were reported as present in two intervals of the succession (= reoccurring taxa, see Table 1). Only in the 16-day turtle carrion study of Abell et al. [16] were some of the taxa (8%) present for five intervals (staphylinid beetles, sarcophagid flies). Therefore, expressing each taxon's appearance as a single interval would capture, at least for modelling purposes, the general pattern of arthropod visitation in these 23 cases.

A taxonomic analysis of all reoccurring taxa, which number 115 in the 18 assemblages, shows that they occur in 6 classes, 12 orders, and 29 families of arthropods and in each of the four ecosystem types (Table 2). After first accounting for the relative contribution of each of the four ecosystem types (tropical and temperate, 34.5% each; desert, 22%; coastal, 9%), temperate and coastal ecosystems appear to harbor disproportionately higher fractions of reoccurring taxa (57% and 14%, respectively) than tropical and desert ecosystems (18% and 11%, respectively). Rove beetles (staphylinids) were the most frequently reported reoccurring taxa (12 cases, Table 2), followed by histerid beetles (8 cases), spiders and flesh flies (araneids and sarcophagids, 7 each), collembolans (spring-tails), muscid flies and other unspecified dipterans (5 each, Table 2). Four instances of reoccurring taxa were found in each of five other arthropod families: carabids (ground beetles), catopids (catopid beetles), silphids (carrion beetles), calliphorids (blow flies) and phorids (humpbacked flies). The 12 taxa listed previously were approximately equally divided among taxa with saprophagous (sarcophagids, collembolans, muscids, calliphorids, phorids) and predaceous (staphylinids, histerids, spiders, catopids, silphids) habits.

Periods of 'absenteeism' recorded among reoccurring taxa ranged from one sample (usually a single day) to 28 samples (a 69-day absence by a rove beetle, Ref 15; see Table 2). Nearly half of the 115 cases in Table 2 (55/115) involve taxa whose appearances and reappearances were separated by only a single sample. Such a high incidence of single-sample absences in reoccurring taxa (48%) begs the question: Would an increase in sampling effort on these days have uncovered previously unseen members of these taxa? Second, if undersampling inflated the number of reoccurring taxa reported in a given study, which taxa went undersampled? Given the lack of detailed information about the distribution over time of sampling effort in these studies, these questions for the present, remain unanswered.

How Does the Taxonomic Composition of the Carrion-Arthropod Community Change Over Successional Time?

One of the dynamic daily changes that occur in and on a carcass are taxonomic shifts in carrion-arthropod taxa. Measures of between-sample similarity in faunal composition, derived from quantitative community ecology [28], were used in this study to quantify daily taxonomic changes in the carrion community. Specifically, this section explores the

use of the Jaccard metric [28 and references therein] for measuring day-to-day changes in faunal similarity for each of the 23 cases.

Methods

The Jaccard metric was chosen among other similarity coefficients because two studies [29,30] judged it to have excellent statistical properties:

$$s_{ij} = a/(a + b + c) \quad (1)$$

where s_{ij} is the degree of similarity between any pair of time-specific samples i and j ; a is the number of taxa common to both samples; b is the number of taxa found in sample i , but not in j ; and c is the number of taxa found in sample j , but not in i . Like most other similarity measures designed for binary-type data, The Jaccard metric ranges in value between zero, when the two samples fail to match on any taxa, to unity, when they match perfectly. For example, in Fig. 1B, s_{ij} for days 1 and 2 is 0.60 ($s_{12} = 3/[3 + 0 + 2]$, using Eq 1). Note that the similarity between samples j and i gives the same value as the similarity between i and j ; thus, all s_{ji} values can be ignored. To obtain the mean similarity for each of i samples (or days) in the succession, \bar{S}_i , the average of the s_{ij} 's are taken over the $N = 1$ samples ($j = s_{i1}, s_{i2}, \dots, s_{iN}$, for all $s_{i \neq j}$; see footnote 2). Finally, the grand mean of the between-sample similarities (S_{gmean}) for a given carrion-arthropod assemblage is calculated as the average of the \bar{S}_i 's, taken over the N samples ($i = 1, 2, \dots, N$; see footnote 3).

Results and Discussion

Several temporal trends emerged in the 23 assemblages. Due to space constraints only 18 of the 23 assemblages (chosen at random from the list in Table 1) are shown in Fig. 2. These results will be reported in qualitative terms.

In most of the 18 cases of Fig. 2, the midsuccessional samples, owing to their higher species richness, were taxonomically more similar to all other pairwise samples, on the average, than early and late successional samples which were poorer in species. These quantitative relationships between early, middle and late successional samples gave the characteristic "horseshoe-shaped" arch in the mean sample similarities (\bar{S}_i 's) in most of the 18 cases. Note, however, that five of the 18 plots in Fig. 2 revealed little or no decrease in mean similarities in the last (right most) samples (Figs. 2A,C,G,O,R). Schoenly and Reid [9] found in two cases studied here (Refs 10,14), that the authors had terminated their observations before large fractions of carrion taxa had emigrated. Arguably, if more

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$$\bar{S}_i = \sum_{j=1}^N s_{ij}/(N - 1), \text{ where } i \neq j \quad (2)$$

For example, the average similarity for sample (day) 1 in Fig. 1B is:

$$\bar{S}_1 = (0.60 + 0.60 + 0.50 + 0.60 + 0.40 + 0.40 + 0.50 + 0.25)/8 = 0.48$$

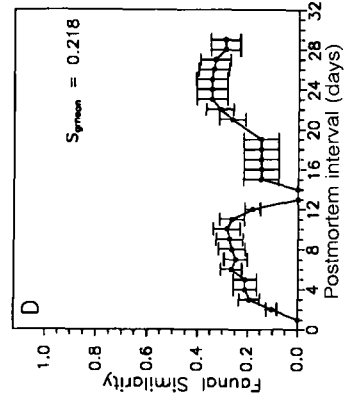
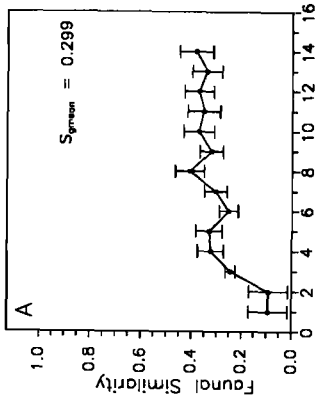
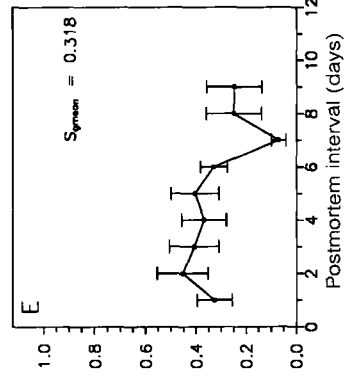
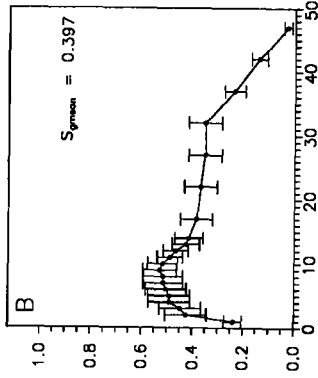
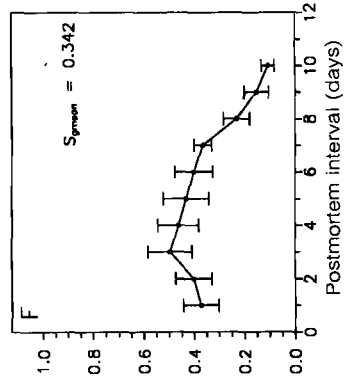
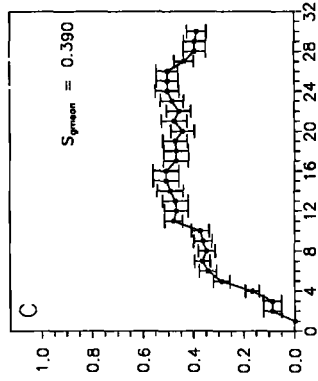
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$$S_{\text{gmean}} = \sum_{i=1}^N \bar{S}_i/N \quad (3)$$

Returning to the example in Fig. 1B, the S_{gmean} is:

$$S_{\text{gmean}} = (0.48 + 0.58 + 0.58 + 0.65 + 0.67 + 0.64 + 0.64 + 0.55 + 0.37)/9 = 0.57$$

Note that like s_{ij} in Eq 1, \bar{S}_i and S_{gmean} in Eqs 2 and 3 take values between 0 and 1.



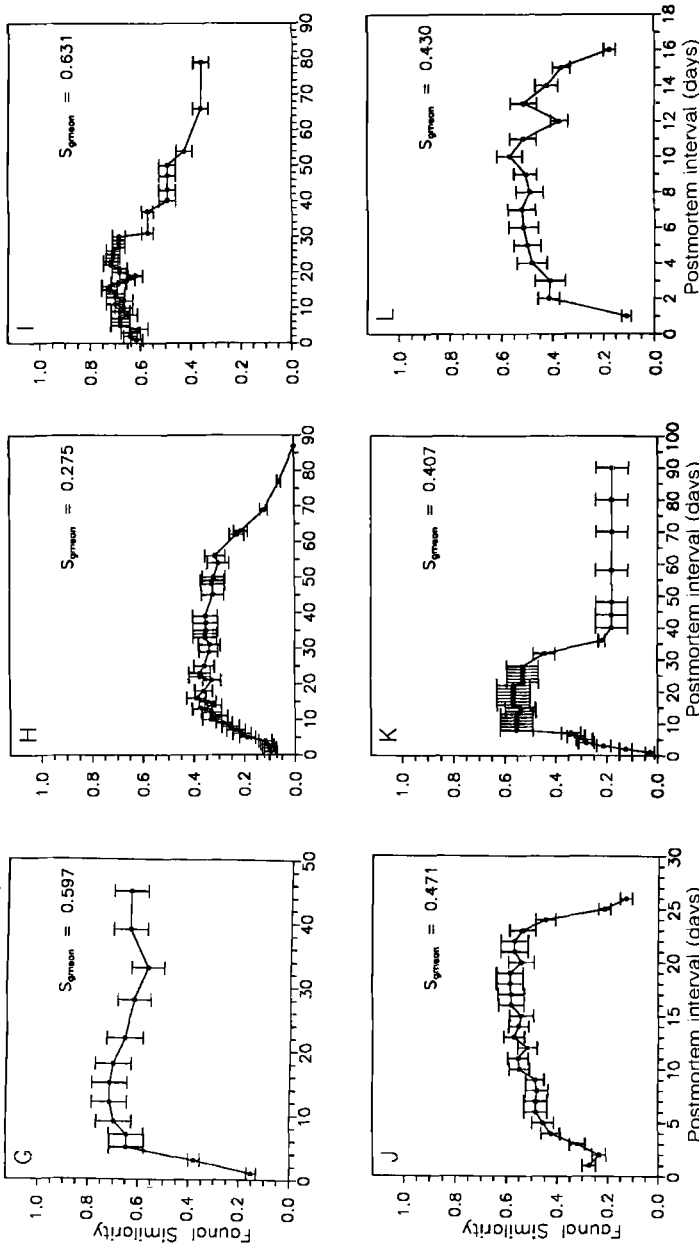


FIG. 2A-R—Plots of mean pairwise similarities (Jaccard metric) for each sample (day) in the succession (vertical error bars are population standard deviations about the mean). The grand mean of the paired-sample similarities (S_{Sympson}) is shown in the upper right corner in each panel (compare with values in Table 1). A, Chapman and Sankey; B, Reed; C, Nabaglo, underground fauna; D, Nabaglo, aboveground fauna; E, Cornaby, Osa toads; F, Cornaby, Osa lizards; G, Johnson; H, Smith; I, McKinney, White Sands; J, McKinney, Hueco Mts.; K, Jirón and Cartini; L, Abell et al.; M, Schoenly and Reid, jackrabbits; N, Lord and Burger, coastal thickets; O, Lord and Burger, cobble beaches; P, Early and Goff, Manoa Valley; Q, Early and Goff, Diamond Head Crater; R, Brauck.

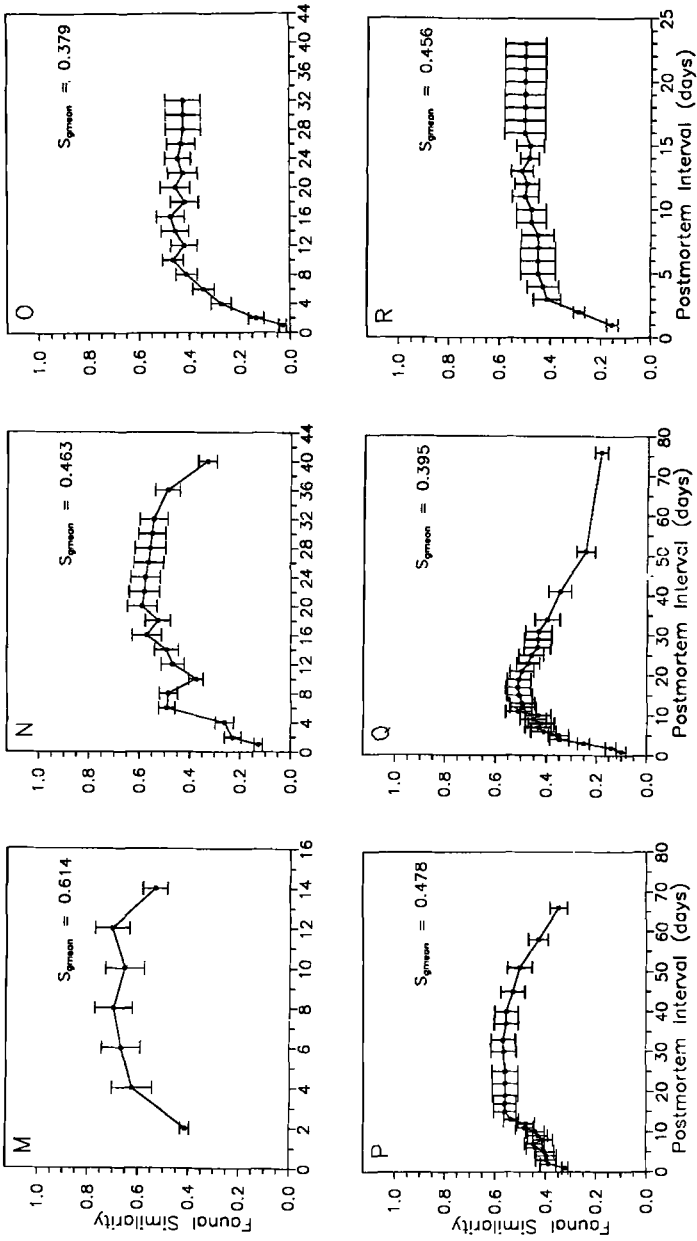


FIG. 2A-R—Continued

time-specific samples had been collected in the five present cases, plots containing these 'extra' samples would likely show a decrease in their mean sample similarities next to the last successional samples.

That the plots of mean-sample similarities in Fig. 2 manifested similar shapes and ranges seems to reflect a general property of the dynamic daily changes that occur during carrion-arthropod succession. However, inspection of *individual* pairwise-similarities in these data sets also show lack of change in taxonomic composition for some periods of the succession. Sample-pairs with matching sets of taxa are hereafter called "matching sample-pairs." For example, in Fig. 1, there are two matching sample-pairs: days 2 and 3, and days 6 and 7. A total of 199 matching sample-pairs were found in 17 of the 23 data sets. Although 199 seems large, this number accounted for only 3.3% of the total number of sample-pairs and, in these studies, ranged from zero (in 6 cases) to 18.2% (Ref 23, Aden Crater site; Table 1).

Most of the 199 matching sample-pairs were found as 'blocks' of consecutive samples. For example, in McKinnerney's White Sands study, four blocks of consecutive samples occur on days 5–7, 11–14, 24–26, and 40–50. These blocks are recognizable in the plot of Fig. 2I as sets of horizontal line segments of connected points sharing the same mean and standard deviation. Other 4-block cases included Jirón and Cartin's study (days 8 to 13, 16 to 22, 23 to 28, 40 to 90; Fig. 2K) and Bornemissza's study (days 4 to 6, 11 to 13, 18 to 22, 24 to 30; not pictured in Fig. 2). The longest single period of consecutive matching sample-pairs was found in Braack's study where a block of 8 taxonomically identical samples were found on days 16 to 23 of the succession (Fig. 2R). Thus, periods of taxonomic 'stasis' in arthropod species composition were generally rare in these reports, but when they occurred they generally persisted for somewhat lengthy periods.

The 199 matching sample-pairs are not evenly distributed along the length of the observation period. If, in each study we divided the total observation period into three equal-sized time periods so as to produce early, middle and late successional intervals and, if the matching sample-pairs are then sorted into these intervals, we find that half (49%) of the matching samples occurred in the late interval, followed by 33% and 18% for the middle and early intervals, respectively. The low numbers of matching sample-pairs in the early interval parallel the period of rapid accumulations of new taxa that typically follows carcass placement. Conversely, the high number of matching sample-pairs found in the late interval parallels periods of low species turnover and richness reported in advanced decomposition and skeletal remains periods. Thus, the species turnover rate and age of the carcass determines the frequency and distribution of matching sample-pairs in the succession.

Trophic (=feeding) shifts among carrion-arthropod species also accompany the dynamic taxonomic changes in the carrion community. In a study of temporal variation in food web structure that included two carrion-arthropod assemblages (Hueco Mountains and White Sands data sets, Ref 23), Schoenly and Cohen [31] found that as time increased, sarcosaprophagous species became more numerous than their predators. These sarcosaprophagous taxa, that at first were prey to predaceous species in the food web, later became top predators after their natural enemies left the carcass. As a result, certain properties of the carcass community food web, such as the prey-to-predator richness ratio and the average food-chain length systematically decreased, whereas, other food web properties, such as the percentage of top predators, systematically increased over successional time.

Do Carrion-Arthropod Assemblages Show Random, Clumped or Uniform Spacing of Their Taxa Over Successional Time?

In this section, I apply an ecological metric used by Poole and Rathcke [32] to quantify the degree to which carrion-arthropod taxa overlap each other in time. In conjunction

with a Monte Carlo test⁴ this method is applied to each of the 23 cases to determine whether carrion-arthropod assemblages show random, clumped, or uniform spacing of their taxa over successional time. Following this and other analyses of arthropod visitation patterns, an underlying explanation of the revealed patterns, for the majority of cases, is proposed. Finally, I show how these methods may be used to detect (or validate claims of) between-site, between-treatment, or between-carcass differences in rates of decomposition.

Methods

For two taxa, i and j , and N samples, the overlap between i and j (o_{ij}) can vary between zero (no overlap) and N (complete overlap). In this sense, o_{ij} is the number of samples in common between taxa i and j . For example, Taxon A overlaps Taxon B of Fig. 1 in three samples (days 2 to 4). Note that the overlap between taxon j and i gives the same value as the overlap between i and j ; thus, o_{ji} values can be ignored. To obtain the total observed overlap for the assemblage of T taxa, O_{obs} , all pairwise combinations of o_{ij} (for all $i \neq j$) are summed (O_{obs} in Fig. 1 is 64).

Figure 3A to C shows three models of succession ("random," "uniform or regular," and "clumped or aggregated") in a hypothetical case involving six taxa and ten time-specific samples. As revealed by the pairwise overlaps computed from the occurrence matrices, note that the "uniform" and "clumped" models represent two extreme departures from the "random" model with overlaps ranging from 33 in the highly "uniform" case to 50 in the highly "clumped" case (Figs. 3B,C). The "clumped" case has the largest pairwise overlap of the three cases because O_{obs} increases when more taxa co-occur in the same set of time-specific samples. Between the O_{obs} values of 33 to 50 in this example, a finite number of slightly different configurations, from less uniform to random to less clumped, are possible.

O_{obs} values, by themselves, have limited utility for statistical testing. Each must be compared against a range of overlaps calculated from a set of occurrence matrices generated at random. The null hypothesis tested in each of the 23 cases is that the pattern of arthropod residence times in the observed occurrence matrix is 'featureless,' that is, the pattern of arthropod residence times in the observed case is statistically indistinguishable from the pattern of residence times in randomly generated matrices. To make the null hypothesis biologically meaningful (and harder to reject), it follows that the random matrices should mirror biological reality and differ only in that feature (that is, pairwise overlap) about which a statistical inference will be drawn. Therefore, each random matrix was constrained to have the same T, N , and residence times per taxon as the corresponding observed matrix, but pairwise overlaps were allowed to vary in each randomization. In this first approximation, each random matrix was also constrained to have 100% nonreoccurring taxa. These constraints determined the general, though not the specific, configuration each randomly generated matrix would take.

After each simulation, the number of pairwise overlaps (calculated in the same way as O_{obs}) was determined from the randomly generated occurrence matrix. At the conclusion of 1000 randomizations⁵ the median and range of the expected overlaps were

⁴With the advent of high-speed personal computers, a class of computer-intensive statistical methods called sampled randomization tests (contemplated six decades ago by R. A. Fisher [33] but impractical *then* to implement) are finding widespread application in the sciences. Monte Carlo simulation is one group of sampled randomization tests in which the original data are randomly recombined n times and pseudovalues of the parameter of interest are calculated from each of the n recombinations to determine whether the observed value deviates markedly from the computer-generated pseudovalues. Its chief application is in cases where tests of significance are made for a statistic in which the form of the expected distribution about that statistic is unknown [34].

⁵One-thousand randomizations were needed because theoretical studies have shown that this number is a realistic minimum for a P of 0.05 and is "almost certain to give the same result as the full distribution except in rather borderline cases with P very close to 0.05" (Ref 34, p. 33).

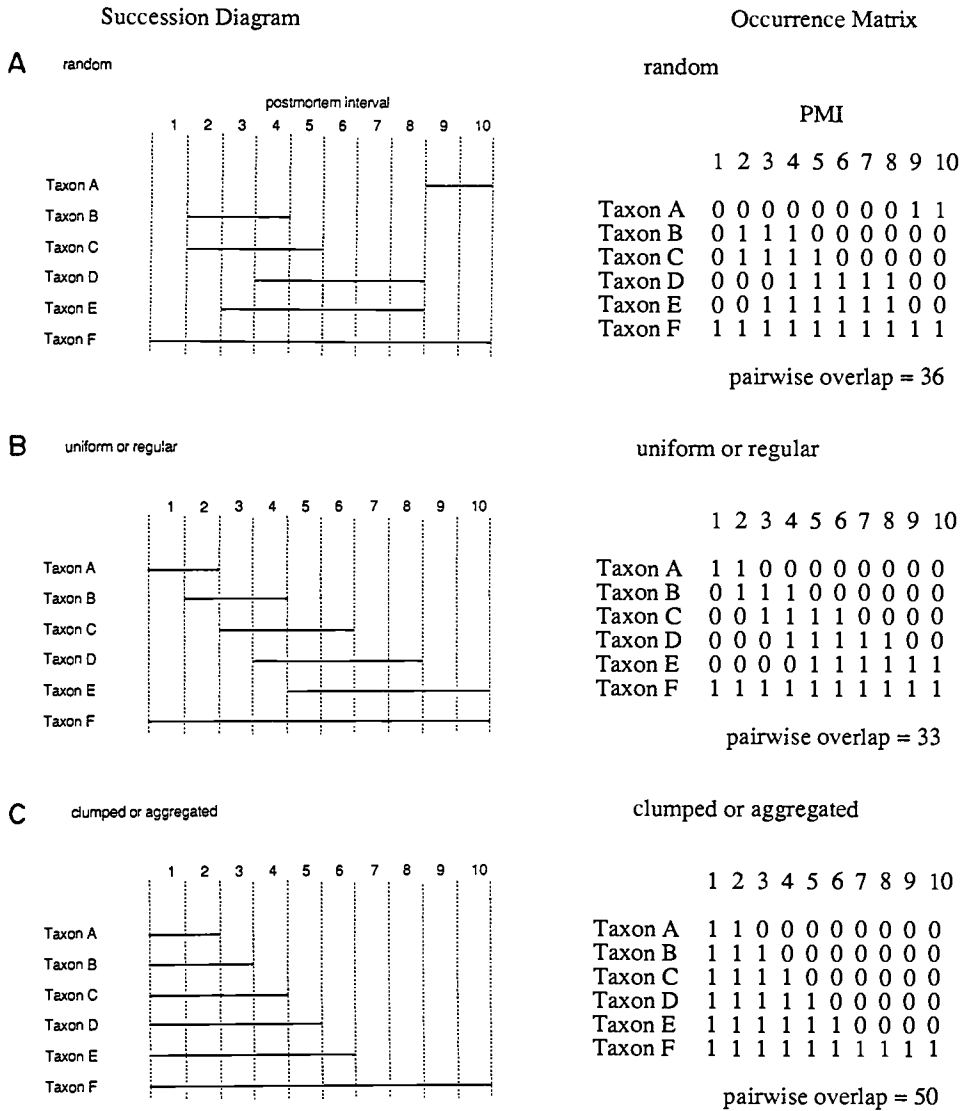


FIG. 3A–C—Three graphical models of carrion-arthropod succession (A, “random”; B, “uniform”; C, “clumped”) with identical numbers of taxa (6, labelled A through F), time-specific samples (1–10 inclusive), and residence times per taxon (2,3,4,5,6,10 samples). In A) arthropod residence times are randomly distributed, B) residence times have uniform or regular spacing, and C) residence times are clumped or aggregated. As revealed by the pairwise overlaps calculated from the corresponding occurrence matrices on the right, note that the “uniform” and “clumped” models represent two extreme departures from the “random” case, with overlaps equalling 33, 36, and 50 in the “uniform,” “random,” and “clumped” cases, respectively.

determined and the probability, *P*, for the null hypothesis was calculated. This process was repeated for each of the 23 assemblages listed in Table 1.

A *P* value for each of the 23 assemblages was calculated as the proportion of random matrices with greater overlap than *O*_{obs}. Following standard acceptance/rejection criteria for a two-tailed test ($\alpha = 0.05/2$ or 0.025), if this *P* value fell outside this predetermined

acceptance region of the null hypothesis ($0.025 \leq P \leq 0.975$), then the null hypothesis was rejected. For each of the 23 cases, the null and alternative hypotheses are:

H_0 : Arthropod residence times display a distribution that is statistically indistinguishable from random expectation ($0.025 \leq P \leq 0.975$).

H_1 : Arthropod residence times display a clumped distribution ($P < 0.025$).

H_2 : Arthropod residence times display a uniform distribution ($P > 0.975$).

Results and Discussion

If the "random" model of arthropod residence times is correct for a given case, the median value of P calculated from 1000 randomizations should be 0.5, with values distributed uniformly over the interval (0,1). That is, random chance dictates that half of the randomly generated matrices should have residence times that are more clumped than the observed case (O_{obs}) with the remaining half showing more uniformly spaced residence times than O_{obs} . If a calculated P value is sufficiently small, it indicates that the distribution of residence times in the observed case follows a "clumped" model of succession; whereas, if a P value is sufficiently large, the observed case follows a "uniform" model of succession.

Seven of the 23 cases in Table 3 showed a statistically significant departure from random expectation. Four of these seven revealed a statistically significant clumped pattern of arthropod residence times (P 's < 0.025): Nabaglo's above-ground case (0.0), Cornaby's Guanacaste toad (0.015) and Guanacaste lizard (0.006) cases, and McKinnerney's White Sands case (0.0, Table 3). A clumped pattern of residence times is also suggested in nine other cases (arranged in order of decreasing likelihood): Cornaby's Osa toads ($P = 0.037$), Schoenly's jackrabbits (0.072), Cornaby's Osa lizards (0.125, Jirón and Cartin's dog (0.186), Lord and Burger's cobble beach case (0.249), Chapman and Sankey's rabbits (0.266), Reed's dog and Nabaglo's underground vole studies (0.424 for both), and Johnson's study (0.426, Table 3). A case-by-case comparison of observed and expected (median) overlaps for each of these 13 clumped cases confirmed an excess of observed overlaps over expected overlaps (means of the medians: 1263 vs. 1186, respectively, Table 3). On the other hand, three of the seven statistically significant cases cited above revealed a uniform pattern of arthropod residence times (P 's > 0.975): Bornemissza's guinea pig study (1.0), Early and Goff's Manoa Valley case (0.980), and Braack's impala study (0.978, Table 3). Uniform distributions are also suggested in seven other cases (arranged in order of decreasing likelihood): Early and Goff's Diamond Head Crater case (0.973), McKinnerney's Aden Crater case (0.832), Lord and Burger's coastal thicket case (0.817), Abell, Wasti and Hartmann's turtle study (0.742), Smith's fox study (0.692), McKinnerney's Hueco Mountains case (0.584), and Schoenly and Reid's cottontail case (0.535, Table 3). A case by case comparison of observed and expected (median) overlaps for each of these ten uniformly spaced cases confirmed an excess of expected overlaps over observed overlaps (means of the medians: 2790 vs. 2665, respectively, Table 3). On the whole, the 23 comparisons of observed and expected overlaps revealed an excess of clumped cases over uniform cases (13 vs. 10, respectively), and within the sets of clumped and uniform cases, examples of statistically significant and marginally significant P values were revealed.

The knowledge that carrion-arthropod residence times are clumped in a majority of cases, does not reveal *when* they are clumped. More specifically, one can ask: Do carrion arthropods typically exhibit a "clumped, early," "clumped, midterm" or "clumped, late" visitation pattern? One solution is to plot newly arriving taxa as a function of time—a species accumulation curve—for both observed and simulated data to determine the pattern of the species accumulation process (that is, early, middle or late) in the observed case relative to the expected version. Newly arriving taxa are defined as the number of

TABLE 3—Results of randomization trials for the 23 cases listed in Table 1 to determine whether arthropod residence times have random, uniform or clumped distributions (order of studies follows the Table 1 arrangement by environment).

Carrion-arthropod assemblage	O_{obs}^a	Randomization Statistics		
		Range ^b	Median ^c	P^d
Chapman and Sankey (1955)	460	384–541	443	0.266
Bornemissza (1957)	9323	9546–10 582	10003	1.000
Reed (1958)	4408	3966–4923	4374	0.424
Nabaglo (1973), underground	2203	1907–2340	2102	0.424
Nabaglo (1973), aboveground	1929	1175–1789	1405	0.0
Johnson (1975)	1618	1515–1703	1614	0.426
Smith (1975)	3235	2930–3872	3305	0.692
Abell et al. (1982)	408	372–492	423	0.742
Cornaby (1974), Osa toads	115	80–133	97	0.037
Cornaby (1974), Guanacaste toads	58	44–65	50	0.015
Cornaby (1974), Osa lizards	576	461–649	540	0.125
Cornaby (1974), Guanacaste lizards	248	214–251	227	0.006
Jirón and Cartin (1981)	815	656–914	772	0.186
Early (1985), Early and Goff (1986); Manoa Valley	4716	4600–5416	4932	0.980
Early (1985), Early and Goff (1986); Diamond Head Crater	2542	2473–3088	2693	0.973
Braack (1987)	677	640–914	747	0.978
McKinnerney (1977, 1978), White Sands	3395	3097–3373	3233	0.0
McKinnerney (1977, 1978), Aden Crater	838	834–857	842	0.832
McKinnerney (1977, 1978), Hueco Mts.	4022	3798–4356	4040	0.584
Schoenly and Reid (1983), jackrabbits	226	205–235	217	0.072
Schoenly and Reid (1983), cottontail rabbits	157	147–177	158	0.535
Lord and Burger (1984), coastal thickets	732	678–850	756	0.817
Lord and Burger (1984), cobble beaches	362	310–414	349	0.249
Clumped cases ($N = 13$), Means:	1263		1186	0.146
Uniform cases ($N = 10$), Means:	2665		2790	0.813

^aObserved overlap (from column 8 of Table 1).

^bThe range of variation in expected overlaps among the 1000 randomizations.

^cThe median expected overlap among the 1000 randomizations.

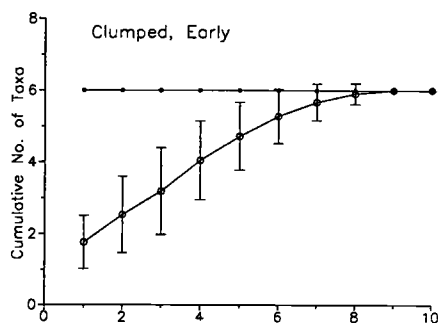
^dThe proportion of randomizations with greater overlap than O_{obs} . A P -value less than 0.5 indicates a clumped distribution of taxa in the observed case; whereas, a P -value greater than 0.5 indicates a uniform distribution of taxa in the observed one. Each random matrix had the same number of taxa (T), time-specific samples (N) and residence times per taxa as the observed case. See text for details.

taxa who were not found in any previous time-specific sample. For the first time-specific sample, the number of newly arriving taxa is equal to the total number of taxa in that sample.

Consider in Figs. 4A to C the three occurrence matrices labelled “clumped, early,” “clumped, midterm,” and “clumped, late” and the resulting observed and simulated species accumulation curves for a hypothetical case of six taxa and ten samples. One-thousand simulations of this occurrence matrix provided the data for the three expected curves (means \pm sample standard deviations, Figs. 4A to C), which served as reference plots against which the observed plots were judged. In Figs. 4A and 4C, note that the observed plots meet but do not intersect the expected plots. The observed plot in Fig. 3A is a straight horizontal line above the expected curve because all newly arriving taxa appeared (early) on day 1; the observed plot in Fig. 4C is nearly the reverse of Fig. 3A, but here the last newly arriving taxon appeared (late) on day 9 (Taxon A). On the other hand, the observed and expected plots of Fig. 4B intersect on day 3, thus reflecting the “midterm” state between the “early” and “late” extremes. Although cases Figs. 4A and

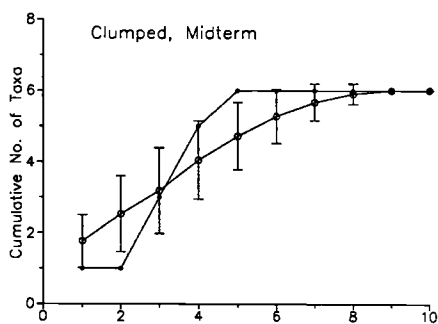
A Clumped, Early

	PMI									
	1	2	3	4	5	6	7	8	9	10
Taxon A	1	1	0	0	0	0	0	0	0	0
Taxon B	1	1	1	0	0	0	0	0	0	0
Taxon C	1	1	1	1	0	0	0	0	0	0
Taxon D	1	1	1	1	1	0	0	0	0	0
Taxon E	1	1	1	1	1	1	0	0	0	0
Taxon F	1	1	1	1	1	1	1	1	1	1



B Clumped, Midterm

	PMI									
	1	2	3	4	5	6	7	8	9	10
Taxon A	0	0	0	0	1	1	1	0	0	0
Taxon B	0	0	0	1	1	1	1	0	0	0
Taxon C	0	0	0	1	1	1	1	1	0	0
Taxon D	0	0	1	1	1	1	1	1	0	0
Taxon E	0	0	1	1	1	1	1	1	1	0
Taxon F	1	1	1	1	1	1	1	1	1	1



C Clumped, Late

	PMI									
	1	2	3	4	5	6	7	8	9	10
Taxon A	0	0	0	0	0	0	0	0	1	1
Taxon B	0	0	0	0	0	0	0	1	1	1
Taxon C	0	0	0	0	0	0	1	1	1	1
Taxon D	0	0	0	0	1	1	1	1	1	1
Taxon E	0	0	0	1	1	1	1	1	1	1
Taxon F	1	1	1	1	1	1	1	1	1	1

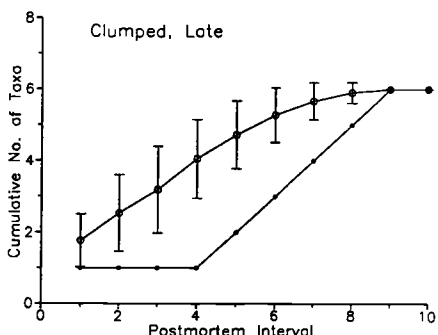


FIG. 4A–C—Three models of clumped residence times among carrion-arthropod taxa (A, “Clumped, Early”; B, “Clumped, Midterm”; C, “Clumped, Late”) with identical numbers of taxa, time-specific samples and residence times per taxon (compare with Fig. 3). Data from the occurrence matrices provided the values for the “observed” species accumulation plots (solid symbol plots) shown on the right; whereas, 1000 simulations of this 6-taxa, 10-sample matrix provided the data for the three identical “expected” species accumulation plots (open symbol plots: mean ± sample standard deviations; see text for further details).

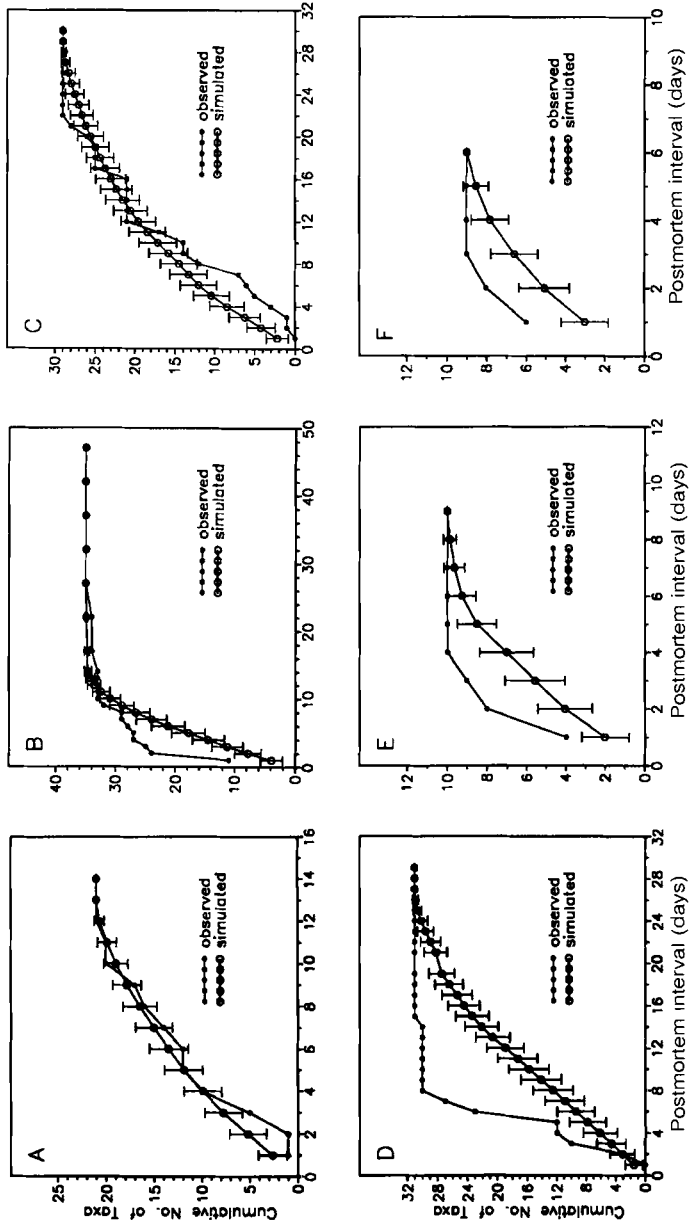
4C are easy to distinguish from one another, deciding between cases 4A and 4B or between cases 4B and 4C is indeterminable from simple visual inspection. Counting the number of observed points that lie above or below the expected points is one way to decide a difficult case.

Comparison of species accumulation curves for observed and simulated data showed that of the 13 “clumped” cases cited in the previous section those following the “clumped, early” model were unequivocal in seven cases (Figs. 5D to G,J,L,M) and intermediate

between “clumped, early” and “clumped, midterm” in two other cases (Figs. 5B,K). Close inspection of these two cases reveals that both are more consistent with the “clumped, early” model than the “clumped, midterm” model, as a higher fraction of observed points lie above than below the corresponding expected points in each plot. The remaining four of the 13 “clumped” cases lie intermediate between the “clumped, midterm” and “clumped, late” models (Figs. 5A,C,H,I). Counts of observed points in these four cases revealed that three were consistent with the “clumped, midterm” model (Figs. 5C,H,I) while a fourth was consistent with the “clumped, late” model (Fig. 5A). It is interesting to note that none of the 13 cases gave unequivocal support for the “clumped, late” model. Thus, the species accumulation curves in these 13 “clumped” cases showed that most (9 or 69%) followed a “clumped, early” model of carrion-arthropod succession. Why should carrion-arthropod taxa, in the majority of these cases, show a “clumped, early” visitation pattern?

Natural selection favors the earliest and most efficient colonizers of a carcass because scavenging (and various abiotic forces) lead to reduction of the carcass [35–37]. A large body of experimental and observational data has shown that organisms that colonize ephemeral and spatially unpredictable microhabitats like carcasses possess different sets of life-history traits than organisms that colonize other types of habitats [reviewed in Refs 37–39]. For example, among adult carrion-frequenting Diptera and Coleoptera, some of the favored traits include: high mobility coupled with an ability to search large areas quickly, a breeding system based on a female-biased sex ratio, and close-inbreeding to increase the reproductive potential of the species and to insure successful colonization of new carcasses [39]. Within the Diptera, sarcophagids (flesh flies) lay first-instar larvae rather than eggs thus giving some species an earlier start on development than egg-laying calliphorids (blow flies) [39]. Among the favored traits that maximize survival of larval Diptera and Coleoptera during development on carcasses, rapid feeding and a high net conversion efficiency may be most important. Individuals that possess these traits can grow to a larger size sooner, which in turn can enhance competitive ability [39] and decrease predation risk [35], compared to lesser-suited individuals. Thus, evolutionary considerations make explicable the finding in this study that carrion taxa, in the majority of cases, show a “clumped, early” pattern of carcass visitation.

It may be possible to use the simulation results of Table 3 and species accumulation plots of Fig. 5 to validate authors’ claims of between-site, between-treatment or between-taxon differences in carcass decay rates. For example, it follows that if a set of carcasses placed at site A are claimed to have faster rates of decay than a second set at site B (observation periods and other features being equal), a more clumped (early) distribution of arthropod residence times should manifest itself on site-A carcasses than site-B carcasses; alternatively, a more uniform (or wider-spaced) distribution of residence times should manifest itself on slower-decaying site-B carcasses than faster-decaying site-A carcasses. In three of four reports examined, this was found to be the case. In their 40-day gull carrion study, Lord and Burger found that carcasses located in coastal thickets decomposed more slowly than those located on cobble beaches (Ref 25, p. 1261). Simulation results for these data indeed showed a more uniform pattern of residence times for the slower-decaying coastal-thicket carcasses ($P = 0.817$) and a more clumped pattern for the faster-decaying cobble-beach carcasses ($P = 0.249$, Table 3). In his 30-day vole carrion study, Nabaglo compared decay rates in aboveground and belowground carcasses during summer, spring and winter and noted large differences in the decay rates of the different treatments, from very slow in spring underground carcasses to very rapid in summer aboveground carcasses (Ref 13, p. 260). Simulation results and species accumulation plots for his underground and aboveground summer faunas revealed a conspicuous clumped-early pattern of arthropod residence times for the aboveground assemblage ($P = 0.0$, Table 3; Fig. 5D) and a less conspicuous clumped-late pattern for



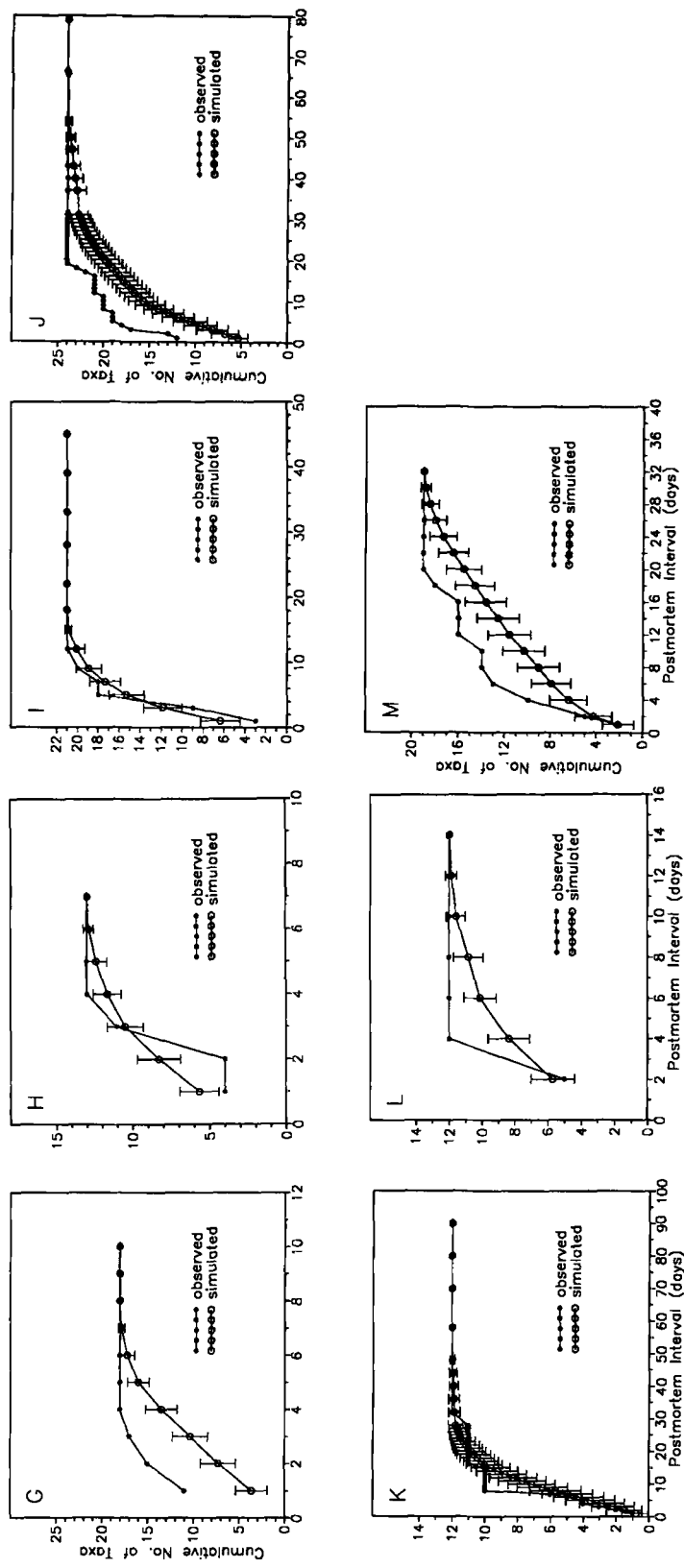


FIG. 5A-M—Species accumulation curves for the 13 “clumped” cases, as revealed by the simulation results in Table 3. Observed data from the 13 occurrence matrices provided the values for the observed plots shown. One-thousand simulations of each observed matrix provided the data for the expected plots shown (general simulation results are reported in Table 3). Error bars are sample standard deviations about the mean. A, Chapman and Sankey; B, Reed; C, Nabaglo, underground fauna; D, Nabaglo, aboveground fauna; E, Cornaby, Osa loads; F, Cornaby, Guanacaste loads; G, Cornaby, Osa lizards; H, Cornaby, Guanacaste lizards; I, Johnson; J, McKinnerney, White Sands; K, Jirón and Carlin; L, Schoenty and Reid, jackrabbits; M, Lord and Burger, cobble beaches.

the underground assemblage ($P = 0.424$, Table 3; Fig. 5C). In his lizard and toad carrion study in Guanacaste and Osa, Costa Rica, Cornaby noted that carcass decay was more rapid at Osa than at Guanacaste and that lizard carrion typically required at least an extra day to decay to the dry skin stage compared to toad carrion at the two sites (Ref 17, p. 52). Simulation results and species accumulation plots for each of Cornaby's four data sets indicated a strong clumped pattern of arthropod residence times (range of P 's: 0.006–0.125, Table 3) and clumped-early visitation patterns in three of the four cases (Figs. 5E to H), however, simulation results did not validate his claims of between-site and between-taxon differences in carcass decay rates. Finally, Schoenly found that jackrabbit and cottontail rabbit carcasses, on average, required 10 and 12 days, respectively, to reach 80% weight loss during summer in the Chihuahuan Desert; thus, jackrabbit carcasses generally decayed at a faster rate than cottontail carcasses at this desert site (Ref 40, Figs. 10 and 11). Simulation results for these two assemblages indeed confirmed the posited relationship between decay rate and arthropod visitation pattern: the faster-decaying jackrabbit carcasses manifested a clumped distribution of arthropod residence times ($P = 0.072$), whereas, a more uniform pattern of arthropod residences were found in the slower decaying cottontail carcasses ($P = 0.535$, Table 3).

Review of Arthropod Successional Patterns and Forensic Implications

1. *In these 23 arthropod assemblages, some forensically-important taxa appear, depart and reappear in the succession (=reoccurring taxa, 20% of all taxa), although the vast majority of arthropod taxa appear and depart over a single time interval (=nonreoccurring taxa, 80%).*

Reoccurring taxa can make PMI estimation more difficult for the entomologist because their known periods of visitation on non-human carcasses may be different from their periods of visitation on human remains or at different sites. Also, period(s) when a reoccurring taxon is present on human remains, when it was found to be absent for the same period(s) on nonhuman carcasses, may be due to incomplete sampling of non-human carcasses. Thus, the recognition that reoccurring carrion taxa exist in different ecosystems, that their numbers may be inflated due to undersampling, and that they occur among forensically important groups (for example, calliphorids, sarcophagids, histerids; see Table 2) are early steps towards factoring in their importance in future entomological investigations.

2. *The midsuccessional faunas, owing to their higher species richness, are taxonomically more similar to all other successional samples, on the average, than the early and late successional faunas which were poorer in species.*

In the 23 data sets listed in Table 1, the grand mean of the paired-sample similarities (S_{gmean}) ranged from 0.218 to 0.808. The range in S_{gmean} may capture most future variation for this statistic because it presently brackets cases involving nonhuman carcasses of different types and sizes placed in different environments.

3. *Over successional time, variability in taxonomic composition is the norm, however, some periods of the succession (especially endpoint samples) show lack of change in arthropod species composition.*

Table 1 revealed that the percentage of matching sample-pairs calculated from the 23 data sets ranged from zero (5 cases) to 18.2% (one case). As in pattern 2 above, this range may capture most future variation for this statistic, since it presently brackets values for 23 heterogeneous cases.

In this study, 18%, 33%, and 49% of the 199 matching sample-pairs came from the first, middle and last thirds of the succession, respectively. The positive trend between the percentage of matching sample-pairs and successional age of the carcass suggests, on

a practical level, that as the actual PMI increases the accuracy of its determination from successional data is likely to decrease because carcasses of advanced decompositional age tend to attract the same set of late-successional species for extended periods. The width of the PMI estimate (the difference between the upper and lower PMI limits) may be a useful metric for quantifying degree of precision (or the confidence interval) of an estimate (hereafter called the PMI_{width}) of the actual PMI. Thus, a narrow-ranging PMI_{width} whose limits bracket the actual PMI (for example, ± 3 days) would, by this definition, be more precise than a wider-ranging PMI_{width} (for example, ± 6 days about the actual PMI), all other factors being equal. The existence of a positive relationship between the PMI_{width} and the actual PMI has not, to my knowledge, been statistically shown from arthropod successional data. Clearly, more between-study comparisons (and more studies) of carrion-arthropod succession in human and non-human cases are needed to test these tentative predictions.

4. *Monte Carlo simulation reveals that the majority of the 23 assemblages (13 or 56%) followed a “clumped” model of species residence times on the carcass, whereas, residence times in the remaining ten cases (44%) followed a “uniformly spaced” model.*

I show how the results of Table 3 and Fig. 5 may be used to detect (or confirm previously claimed) between-site, between-treatment or between-taxon differences in carcass decay rates. The use of Monte Carlo methods and species accumulation plots supplements other approaches that have been used to detect differences in carcass decay rates (for example, decay stage duration versus species diversity; see Ref 25). Beyond comparison of visitation patterns and decay rates, it is also of forensic interest to consider a taxonomic study of the *sequence* of arthropod arrival times on carcasses.

Most of the 13 “clumped” cases of arthropod visitation were found to be consistent with findings from the evolutionary biology literature. Biological and environmental correlates for the “uniformly spaced” visitation pattern found in the 10 remaining cases, however, were not addressed in this study. These and other open questions remain to be resolved by future experimental and statistical work in this area.

5. *Comparison of species accumulation curves for observed and simulated data showed that of the 13 “clumped” cases cited in 4 above, most (9 or 69%) followed a “clumped, early” model of carrion-arthropod succession (rather than a “clumped, midterm” or a “clumped, late” model).*

The prevalence of the “clumped, early” pattern underscores the dynamic nature of carrion-arthropod succession and the speed to which maximum species richness can be attained on carcasses. For example, the panels of Fig. 5 show that, on the average, peak taxonomic richness occurred 12 days sooner in the 13 observed versions (mean: 13 days, range: 4 to 22 days) than the corresponding expected (simulated) versions (mean: 25 days, range: 6 to 79 days). Beyond using early-successional indicators (that is, calliphorid and sarcophagid flies), entomologists should consider recruiting a richer diversity of taxa, whenever possible, in their PMI estimation procedures (for example, beetles and mites; for applications see Refs 27,41,42). Such recruitment brings two advantages: an opportunity to extend the range of days for PMI estimation⁶ and the likelihood of increased accuracy of the PMI estimate.^{7,8}

6. *Keeping in mind the possible practical limitations of using nonhuman carrion-arthropod data to predict the PMI in human remains cases, the methods and results detailed in this study, nevertheless, provide an early step towards development of statistical protocols, sensitivity tests of baseline data, and baseline limits in forensic entomology.*

⁶M. Lee Goff, personal communication, July 1991.

⁷M.I. Marchenko, personal communication, 1 August 1991.

⁸K. Schoenly, unpublished data.

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