

Decay and Disarticulation of Small Vertebrates in Controlled Experiments

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A study was conducted to examine the timing and nature of decay and disarticulation in small vertebrates, using an experimental regime that allowed comparison among different environments, and different size classes of amphibians, reptiles, birds, and mammals. Decay and disarticulation of freshly killed small vertebrates was documented in freshwater and seawater aquaria as well as outdoor terrestrial settings protected from scavengers by partially buried cages. Experimental animals included salamanders (two sizes), lizards, finches, doves, mice, rats, squirrels, and rabbits. The study area was hot and dry (southern California), with scattered winter rains. Some specimens of each species in the terrestrial environment were transferred after about one month to one of two other environments - freshwater, or an outdoor terrestrial cage simulating increased rainfall. In water the carcasses' flesh decayed by bacterial action in one to six months, but insect larvae removed the flesh from terrestrial carcasses within two weeks, leaving dry, desiccated carcasses that changed little over a four to 11 month period. The process of decay and disarticulation was greatly affected by differences in properties of the skin between species and the reaction of each type of skin to drying or water saturation. Disarticulation time was shortest in water, followed by the high rainfall treatment, then dry terrestrial environment. The sequence of disarticulation varied considerably, especially in the terrestrial treatment, but heads and limbs tended to separate from the body first, and then individual bones separated from the limbs. Also, the pattern of tooth loss or cracking differed among environments. These data provide an actualistic analogue to assist in the interpretation of some parameters of fossil assemblages, including maximum time between death and burial of partially or fully articulated small vertebrate fossils (about 3 months in water, but over a year in dry terrestrial conditions), or the likely paleoenvironment in which an assemblage accumulated.

Keywords: TAPHONOMY, VERTEBRATE, DECAY, DISARTICULATION, BIOSTRATINOMY, EXPERIMENTAL TAPHONOMY

Introduction

The timing and sequence of carcass decay and disarticulation has been studied for a variety of taxa in a number of different settings. Among large vertebrates, disarticulation sequences of ungulate mammals were studied in savannahs (Hill 1979; Hill and Behrensmeyer 1984) and ungulates and a coyote (*Canis latrans*) in more arid environments (Toots 1965). Decay and disarticulation patterns have also been reported for several large ungulate mammal species, as well as large reptiles and fishes in freshwater lake and nearshore habitats (Weigelt 1989). Schäfer (1972) collected considerable data on taphonomy of modern marine vertebrates. Small vertebrate species have also been subjects of actualistic taphonomic studies in a variety of settings (Dodson 1973; Bickart 1984; Oliver and Graham 1994; Davis and Briggs 1998).

These previous studies provide considerable data on sequences of decay and disarticulation of various taxa in a variety of environments. However, few were performed under controlled circumstances allowing the evaluation of taphonomic effects of specific treatments or conditions. Moreover, sample sizes were small, limiting evaluations of pattern variability. Our experiments under controlled conditions designed to reflect natural environments differ from previous research on small vertebrate taphonomy in several ways. 1) Four classes of small vertebrates were studied, in different size categories, under the same experimental conditions, so that the data from all taxonomic and size groups can be compared. 2) Freshwater, seawater, dry

terrestrial, and wet terrestrial conditions were utilized, with other parameters being the same, so that the different treatments are similar. 3) Large sample sizes allowed evaluation of individual variation in the disarticulation process, under similar conditions. 4) These experiments excluded macro-scavengers (larger than insects) to provide a modern analogue of decay and disarticulation processes without the complicating effects of scavenging.

Our experimental data on the timing and qualitative features of decay and disarticulation of small terrestrial vertebrates contributes a baseline analogue for comparison with observations in natural settings. Our goal is to identify taphonomic evidence with potential to assist in interpreting fossil assemblages. Such evidence may indicate maximum and/or minimum time between death and burial, or in what environment the decay and disarticulation process occurred (e.g. in water, on dry ground, or in a wet terrestrial setting). Our conclusions are based on observations of disarticulation events as evidenced by times when body parts or individual bones separated from each other, and on observations of the decay processes.

Materials and methods

Experiments and apparatus

Experiments were conducted in aquaria in a storage building on the Loma Linda University farm, and in outdoor cages on the south side of the building. In the first set of experiments (treatments [Trs.] 1 and 2) (Table 1) all carcasses were in aquaria at approximately room temperature (mean =

21-26° C; Figure 1), Tr. 1 in freshwater and Tr. 2 in seawater. The seawater was produced with Instant Ocean artificial seawater salts, mixed to approximate normal ocean salinity of 34.7 ppt. In the second set (Trs. 3-7) temperature was not controlled; treatments were exposed to the outdoor southern California temperature (ambient temperature hereafter; Figure 2). The second set of treatments included repetition of the freshwater and seawater experiments from Trs. 1 and 2 (now as Trs. 3 and 4) as well as three different outdoor, terrestrial treatments. Carcasses in all terrestrial treatments remained on dry ground for a minimum of 36 days. Some carcasses remained on dry ground for the duration of the observations (Tr. 5). Other carcasses remained on dry ground for 36 days (salamanders only) or 53 days (± 1 day) and were then transferred to either a wet terrestrial environment (Tr. 6 - "wet cage") or a freshwater aquarium (Tr. 7). Specimens for these treatments were chosen (after visual inspection) so that each treatment contained carcasses in approximately the same state of decay and disarticulation on the day of the transfer. Tr. 7 simulated death in a terrestrial environment followed by transport into a stream or lake. Tr. 6 simulated an environment with higher rainfall. Ideally the carcasses in Tr. 6 should have been in the wetter environment during the whole experiment, but observations made during the first 36 days of the study led us to decide that observations in a wetter environment were also needed, so they were begun on day 36 or 53.

Two size classes each of salamanders and birds and three size classes of mammals were used in the experiments

(Table 1, 2). Only one size category of lizard was used because it was not feasible to acquire adequate numbers of a larger species. The species of small salamander varied in different treatments (Table 2), due to changes in availability because of season and changes in collecting regulations. Tr. 1 used laboratory mice and rats and domestic dwarf rabbits, but in Trs. 2-7 wild caught mice, wood rats, and ground squirrels were used, of about the same size as the animals in Tr. 1. Two species of lizard were used in most treatments, with one specimen of a third lizard species in Tr. 1 (Table 2).

Experimental Setting

Trials were conducted in 13 small and three large aquaria. A drain hole cut through the glass near the top of each aquarium controlled the water volume at 57 liters (15 gallons) in the small and 255 liters (67 gallons) in the large aquaria. A cone of window screen covered each drain, preventing loss of carcass parts. Each large aquarium was divided in half by window screen.

Water from the aquarium drains was filtered to keep the water clear, and reduce the unnatural buildup of bacteria. It was then pumped to a holding tank and flowed into plastic tubing that delivered 20 liters of filtered water per hour to each 57 liter aquarium and 40 liters per hour to each 255 liter aquarium. During Trs. 2-7 a 35 W, 107 cm UV sterilizer was installed in the line that carried filtered water to the aquaria.

During Trs. 3 and 4 the aquaria were divided into 13 freshwater (10 small and three large) aquaria connected to the filter system described above, and three small

Table 1. Outline of experiments, with size classes for amphibians (SS and LS = small and large salamander), birds (SB and LB = small and large bird) and mammals (SR, MR, and LR = small, medium, and large rodent or rabbit), sample size (N), and mean weight in grams (M) for animals used in each treatment. Tr. 1: 12/1992 to 4/1993; Tr. 2: 5/1993 to 8/1993; Tr. 3-7: 3/1994 to 4/1997. * Carcasses were transferred from the terrestrial regime to wet cage or freshwater after 36 days (salamanders), or 53 days.

Treatment →	Room temp. ~21-27° C				Ambient temperature = outside air temperature 8-37° C									
	1		2		3		4		5		6		7	
	Freshwater		Seawater		Freshwater		Seawater		Terrestrial		Terrestrial, transferred to wet cage*		Terrestrial, transferred to freshwater*	
Species	N	M	N	M	N	M	N	M	N	M	N	M	N	M
Small salamander	10	5.7	9	4.9	-	-	-	-	6	9.3	2	10	2	8.8
Tiger salamander	9	44	10	36	4	76	4	79	6	89	2	90	2	88
Lizard	10	20	10	20	4	32	4	19	6	24	2	18	2	28
Zebra finch	10	12	10	11	-	-	-	-	6	12	2	13	2	11.5
Ring-necked dove	10	139	10	148	4	148	4	157	6	157	2	155	2	160
Mouse	10	22	10	17	-	-	-	-	6	17	2	17	2	17.5
Rat	10	144	10	152	4	163	4	164	6	170	2	116	2	121
Squirrel/rabbit	5	678	5	656	4	645	-	-	3	623	1	453	1	623

seawater aquaria with a separate filter system and a 0.3 m long UV sterilizer. Plastic tubing carried 46 liters of filtered water per hour to each seawater aquarium.

An east-facing window was partly open during all experiments to allow insects to enter and leave the room at will, and a small fan in this window helped circulate the air. A heating and air conditioning system maintained an approximately constant room temperature during Trs. 1 and 2 (Figure 1). To make Trs. 3-7 as similar as possible, the room was not heated or air conditioned, and the open window allowed the temperature in the room to track the outdoor temperature (Figure 2).

The outdoor experiments were conducted in cages 0.91 m by 0.91 m by 0.5 m high, completely enclosed with 1.3 cm mesh hardware cloth. A hinged top on each cage provided access. Cages were placed in 5 cm deep trenches, and the bottom wire was covered with 5 cm of soil. This experimental area was exposed to ambient temperature and rainfall, except for a few times when part of the area was soaked by malfunctioning sprinklers in an adjacent field.

For Tr. 6 one cage was fitted with mini garden sprinklers to simulate a wetter environment. The sprinkler system was controlled by a timer, that watered this “wet cage” twice a week, for two hours each time, during the early morning. Each two-hour watering session spread approximately 9 cm of water over this area.

These experiments excluded predators and scavengers except for insects and, in the outdoor experiments, anything small enough to go through the 1.3 cm mesh. We did not see evidence of mice in the terrestrial cages.

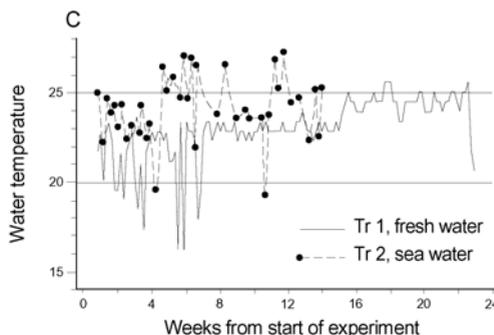


Figure 1. Mean water temperature in Trs. 1 and 2.

Experimental Procedure

Specimens (Table 2) collected in the wild or purchased from animal dealers, were euthanized with ether (according to a protocol approved by the Loma Linda University animal care committee). They were then weighed and placed in one of the experimental treatments, and observed until disarticulated. Each aquarium or outdoor cage contained several carcasses. Data were collected at the following intervals: Trs. 1 and 2 - daily; Trs. 3-7 - two to four times a week for the first eight weeks, once a week from week 9 - 47, once every two weeks from week 48 -71, once a month from week 72 - 131, and every three months thereafter.

Data collection consisted of taking notes on each carcass's condition, the presence of insect activity, state of decay, any body parts that were disarticulated (not attached to the body), and any other pertinent observations. Whenever single bones, separate from the body, were found they were collected, placed in plastic bags, and labeled with the animal number and date of collection. Separated body parts

Table 2. Species of animals used in the taphonomy experiments. (SS and LS = small and large salamander; SB and LB = small and large bird; SR, MR, and LR = small, medium, and large rodent or rabbit).

Common Name	Genus and Species	Treatment
Marbled Salamander (SS)	<i>Ambystoma opacum</i>	1
Blue-spotted Salamander (SS)	<i>Ambystoma opacum</i>	2
Western Newt (SS)	<i>Taricha torosa</i>	5-7
Tiger Salamander (LS)	<i>Ambystoma tigrinum</i>	1-7
Granite Spiny Lizard	<i>Sceloporus orcutti</i>	1-7
Western Fence Lizard	<i>Sceloporus occidentalis</i>	1-7
Alligator Lizard	<i>Gerrhonotus multicarinatus</i>	1
Zebra Finch (SB)	<i>Poephila guttata</i>	1, 2, 5-7
Ring-necked Dove (LB)	<i>Streptopelia risoria</i>	1-7
Laboratory Mouse (SR)	<i>Mus musculus</i>	1
White-footed Mouse (SR)	<i>Peromyscus sp.</i>	2, 5-7
Laboratory Rat (MR)	<i>Rattus norvegicus</i>	1
Desert Wood Rat (MR)	<i>Neotoma lepida</i>	2-7
Domestic (dwarf) Rabbit (LR)	<i>Oryctolagus cuniculus</i>	1
California ground Squirrel (LR)	<i>Spermophilus beecheyi</i>	2, 3, 5-7

containing several bones were left in place so that further disarticulation could be documented. The dated bags of bones and the notes on disarticulation of larger body parts were the principle data for the experiments.

The necessary data could not be collected without some disturbance to the carcasses, but disturbance was kept as uniform as possible across all experimental conditions and animal types. The water in aquaria was stirred with a stick moved in three to four circles of the aquarium, with the amount of movement being approximately the same each time. The stirring was usually fairly gentle, to avoid breaking apart the carcasses. However,

when only mammal skulls and dentaries remained, the water was stirred with enough vigor so that water currents lifted the skulls and moved them around the aquarium. Carcasses lying on the aquarium bottom were lifted to determine if any loose bones were present. In the outdoor cages, each carcass was lifted off the ground during each data collection period, any loose bones were removed, and then the carcass was put back in its original position.

Observations in the aquaria posed particular problems because the decaying carcasses made it difficult to keep the water clear enough to collect data accurately. The filter system helped to clear the water, but hair, feathers, and other debris collected on

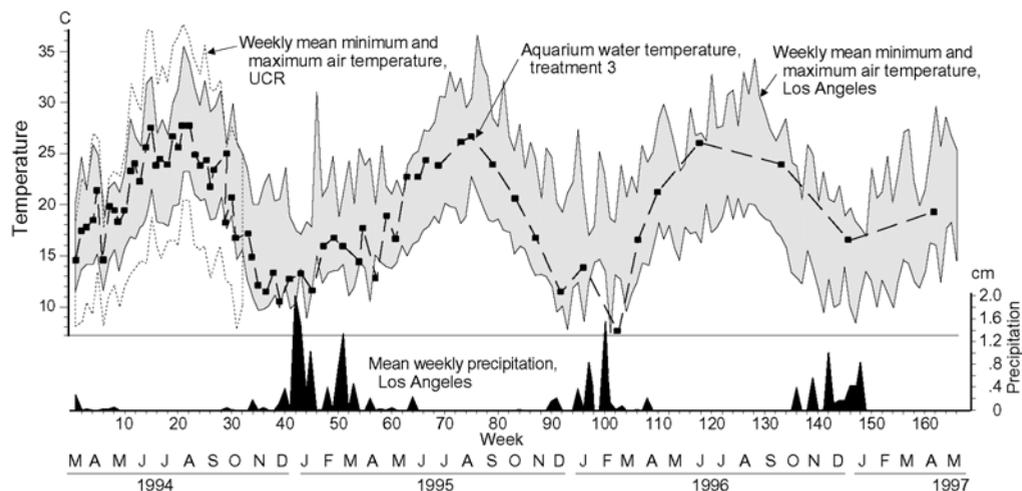


FIGURE 2. Mean weekly weather parameters at local weather stations. The Los Angeles station was 105 km west of the study area. For the first seven months the same parameters at the University of California at Riverside (11 km southwest of the study area) are also shown for comparison. The UCR station was then closed. The central dotted line is the mean water temperature in Tr. 3, collected each time data were collected (water temperature was the same in Trs. 3, 4, and 7). Comparison from Los Angeles and a previously operating weather station 4 km from the study site, for 1965 and 1970, indicates that the amount and annual pattern of precipitation in the two areas is approximately the same.

the aquaria bottoms, and the water became cloudy, making observation difficult. Several methods were used to clean the water. During Tr. 1 some smaller bones were lost while siphoning dirty water out of an aquarium, even though the water was drained through a screen. In Tr. 2, 3, 4, and 7 loss was reduced by use of a small net and a small aquatic vacuum cleaner that pumped water through a fine-mesh cloth bag. The vacuum cleaner was not operated in close proximity to carcasses, to avoid pulling bones loose from the carcasses. Freshwater aquaria were cleared by running water into the aquarium and letting the dirty water run out the aquarium drain, bypassing the filter. This did not result in loss of bones. This process could not be used in seawater

aquaria because it would have changed the salinity. Consequently it was more difficult to keep the seawater clear enough for effective data collection.

Weather, Water, and Soil Conditions

Weather information was obtained from the nearest weather station (Figure 2). The Southern California weather pattern consists of dry, hot summers and cooler winters with occasional rainstorms during fall through spring.

Readings were taken of pH and bacterial levels in the aquaria. Bacteria counts were taken by stirring the water and taking samples from about one inch below

the surface with a sterile container. These samples were plated out at 10:1 and 100:1 dilutions on 1.5% agar gel, incubated for 24 hours, and counted for number of colonies.

Water in all aquaria was basic, with a pH range of 7.9-8.8. During seawater experiments salinity decreased from 35.6 to 18.9 ppt because of loss of salts (normal seawater = 34.7 ppt). Bacteria levels varied from one to 126,000/ml, with the highest counts early in the experiments when a large biomass was decaying. This range is wider than is usual in natural lake water, but most aquaria bacteria counts were within or lower than normal bacteria levels in lakes, which are typically between 10^5 to 10^6 per ml of water (Barnes and Mann 1991). The soil is silty loam and has a pH of 7.5.

Data analysis

The following data were entered into a database: length of time (in days) for each bone and body segment to disarticulate, and amount of time (in days) for each carcass or significant part thereof to sink to the bottom of the aquarium. "Disarticulation time" was calculated, and here refers to the week in which all bones in a taxon were disarticulated (total disarticulation time), or all of a specific bone or bone group. Other calculations and statistical tests are described in Table 3.

Results

Results are based on 17,400 bones and 552 mammal teeth (teeth from Trs. 3-7 only) recovered (Table 4). In the freshwater and seawater treatments, recovery rate was

highest in Trs. 3 and 4, because of the more effective methods used for keeping the water clean. We considered the recovery rates in Trs. 3-7 adequate for reliable analysis of disarticulation times and also disarticulation sequence for specific bones. However, we used data from Trs. 1 and 2 only for analysis of overall disarticulation times because of the lower number of bones recovered.

Decay Process

In fresh or seawater many carcasses floated for a time before sinking (Figure 3). Amphibians floated only for a few days, but lizards seem to be close to the density of water, and floated up and down in the water column for up to 21 weeks. Mammals often sank for the first few hours or days and then floated for a month or more. Some squirrels floated until virtually all bones had dropped off and only a mass of skin and hair was floating. Birds did not sink until they were falling apart, after one or two months.

The processes following death differed across treatments. In water bacterial decay gradually degraded the flesh. Insect larvae infested floating carcasses and caused some damage on the surfaces above water, but their activities were limited. In the terrestrial environment insect larvae quickly removed the flesh of each carcass within a maximum of 6-14 days, leaving only dried skin and bones. These desiccated remains persisted for a long time before beginning to disintegrate. After about two months the skin of small salamanders was largely consumed by small invertebrates. The dry skin of birds, mammals, and large salamanders changed

Table 3. Calculations from the disarticulation data, and statistical tests

Calculations from above data, for each bone type or bone group in each taxon:

Medians - number of weeks until 50% of disarticulation events (bones or body parts separating from body) had occurred.

Quartiles - number of weeks until 25% and 75% of disarticulation events had occurred.

Ranges of weeks for first and last disarticulation events.

Statistical tests:

1. Significance of differences in disarticulation times - Kruskal-Wallis and Mann-Whitney tests using SPSS 10.0 (Norusis 2000).

Median disarticulation time, time at 25% disarticulation, and time at 75% disarticulation were tested separately, using data from all individuals in the taxa being compared.

2. Similarity of disarticulation sequences among species or treatments - nonparametric Kendall's coefficient of concordance (W) (Zar 1984; Nunn and Smith 1998), which tests whether there is concordance (i.e. correlation) between multiple sets of ranked data.

Nonparametric ranks for a set of disarticulation events (disarticulation of specific bones or bone groups) was calculated for each taxon, and the concordance of these sets of ranked disarticulation sequences was tested.

An increase in the number and magnitude of sequence differences yields lower values of W and chi square, and higher *p* values.

The null hypothesis (H_0) is that the sequences are different among species or treatments, and H_A is concordance of sequence among groups (disarticulation sequence does not differ), which we accepted if $p < .05$.

This statistical test allows calculation of W for an entire data set or for individual groups (species or treatments) separately (see Nunn and Smith 1998 for further discussion of the use of this statistic in evaluating sequence data).

This analysis used data on the week of disarticulation of the following body segments or groups of bones (with data from a bone group pooled): skull bones, bones of pectoral girdle, front limb separation from body, bones of front limbs, bones of pelvic girdle, back limb separation from body, bones of back limbs, bones of pes and manus.

Degrees of freedom in this test is based on number of parameters compared, in this case one less than the number of bone groups listed above.

very little for seven to 11 months, even though some bones fell from breaks in the skin before that time. The disintegration of their skin occurred primarily during the rainy season.

Tr. 7 carcasses were placed in water on day 36 (salamanders only) or 53. The dry skin of these desiccated carcasses, with no internal body tissues, was quickly softened by water saturation and the

skeletons fell apart, often in a shorter time than those that were in water from the beginning.

There were important differences in the decay and disarticulation process between major taxonomic groups, and one important controlling factor was the nature of their skin. Salamander skin out of water dried within hours to a very hard, rigid substance, and the skin of large salamanders

did not soften for 11 months, even though it was occasionally wetted by rain. It began to soften and disintegrate during the heavier winter rains. However, salamander skin immersed in water disintegrated quickly, and the skeleton also fell apart quickly. Lizard skin, when dry, was moderately durable, and began to disintegrate after 5-8 weeks. Lizard skin in water formed a limp but durable bag containing the bones. After the flesh decayed this limp bag remained, and was easily moved about by gentle water currents. Many bones fell out through natural openings or breaks in the skin, but individual lizard limbs with the leg bones approximately in position of articulation remained for up to 77 weeks in freshwater.

The durability of bird and mammal skin varied with animal size. In the dry terrestrial environment (Tr. 5) mouse and finch skin was mostly gone within six months, but disintegration of dove, rat, and squirrel skin occurred primarily during the rainy season, 8-15 months into the experiment. In water (Tr. 3) at least part of the skin of birds and mammals lasted through much of the disarticulation process, but breaks in the skin allowed bones to readily fall out.

Disarticulation Time

Differences in disarticulation time across Trs. 3-7 were significant for all species (Table 5B), and disarticulation time varied

Table 4. Recovery rate of bones, as percent of expected number of bones (based on number of bones in each taxon, and number of complete carcasses of that type), listed as range of percentages for different treatments.

	Trs. 3-7	All treatments
Foot bones	17-47	6-47
Ribs and vertebrae	62-82	23-82
Limb and limb girdle bones	80-92	50-92
Skull bones	60-74	60-76
Teeth	88-98	-

with environment and with body size. The shortest disarticulation times for all species occurred in fresh or seawater (5 weeks to 6 months) (Trs. 1-4, 7; Figures 3, 4). Slowest disarticulation occurred in the terrestrial environment (Tr. 5), and it was intermediate in the high rainfall terrestrial environment (Tr. 6). The only exceptions to this pattern (Table 5a; Figure 3b, c) involved lizard limbs and a few dove synsacrum and skull bones in freshwater that took a long time to disarticulate.

In terrestrial conditions disarticulation time increased with carcass size (Tr. 5; Fig. 4a) for salamanders, birds, and mammals, and these differences were significant (Table 5d). In contrast, size had little or no effect on most disarticulation

FIGURE 3. Mean disarticulation times for the large salamanders, lizards, doves, and rats. Black bars indicate percent of bones disarticulating in each two-week interval, and shaded polygons indicate cumulative percent of bones disarticulated, ending at 100% disarticulation. Smaller black bar graphs near top of each aquatic treatment graph indicates percent of carcasses floating during part or all of each two-week interval. Arrows indicate time at which carcasses in Trs. 6 and 7 were transferred from terrestrial to wet or aquatic treatment. Small vertical bars along top of polygons indicate time at 25% and 75% disarticulation.

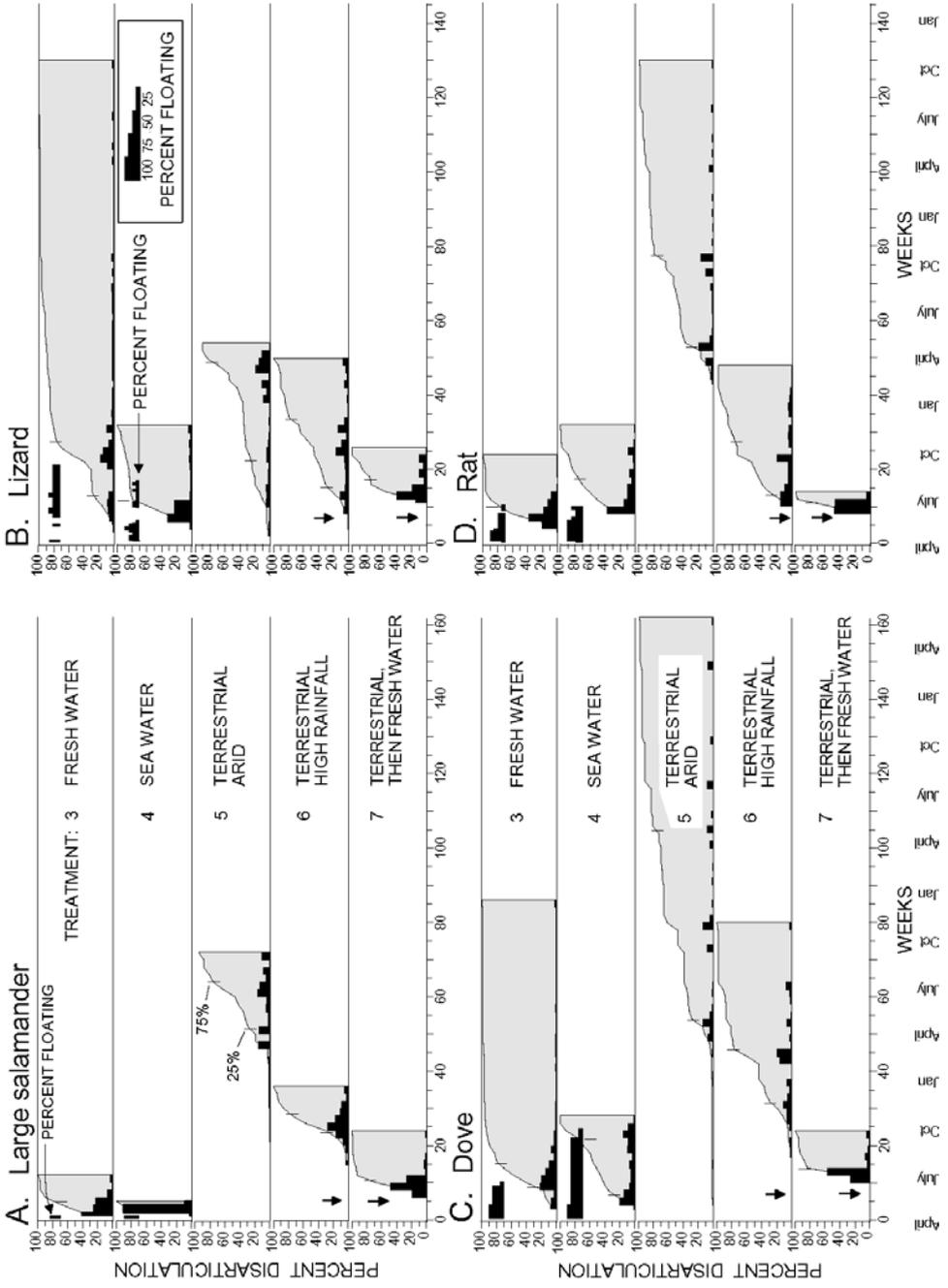


Table 5. Results of statistical tests, showing significance of differences between species or between treatments in disarticulation time. Med = median; KW = Kruskal Wallance test; MW = MannWhitney test; St = statistic (U for MW, Chi Square for KW); "4 classes" in species column indicates large salamander, lizard, dove, rat; Sig = significance: * = significant at 0.05 level; ** - significant at 0.01 level.

Treatment	Species	Test	Df	25%		Med		75%	
				St	Sig	St	Sig	St	Sig
Differences across treatments									
<u>A. Freshwater and seawater treatments</u>									
1-4	Lg sal	KW	3	9.61	.02*	7.27	.06	7.53	.06
1-4	lizard	KW	3	5.84	.12	11.39	.01**	11.51	.009**
1-4	dove	KW	3	7.63	.05*	6.40	.09	6.49	.09
1-4	rat	KW	3	8.33	.04*	7.60	.06	6.69	.08
<u>B. Treatments 3-7</u>									
3-7	Lg sal	KW	4	13.06	.01**	12.70	.01**	12.76	.01**
3-7	lizard	KW	4	4.95	.29	10.61	.03*	11.60	.02*
3-7	dove	KW	4	12.10	.02*	11.98	.02*	12.29	.02*
3-7	rat	KW	4	12.84	.01**	12.50	.02*	12.40	.02*
3, 5	sq	MW		.000	.03*	.000	.03*	.000	.03*
Differences between species									
<u>C. Comparison of lizard species</u>									
3	lizards	MW		1.00	.44	2.00	1.00	.00	.12
5	lizards	MW		2.00	.56	.50	.20	2.50	.77
<u>D. Terrestrial</u>									
5	all	KW	7	14.81	.04*	16.04	.03*	16.04	.01**
5	sals	MW		.00	.006**	.00	.006**	.00	.006**
5	birds	MW		.00	.004**	.00	.004**	.00	.004**
5	mammals	KW	2	11.94	.003**	11.83	.003**	10.75	.005**
<u>E. Freshwater treatments</u>									
1	birds	MW		40.50	.47	40.00	.45	37.50	.34
1	mammals	KW	2	.35	.84	4.81	.09	9.44	.009**
3	rat, sq	MW		5.50	.47	6.00	.69	8.00	1.00
7	4 classes	KW	3	6.17	.10	6.53	.09	6.53	.09
<u>F. wet cage (high rainfall)</u>									
6	4 classes	KW	3	5.44	.14	6.11	.11	4.50	.21

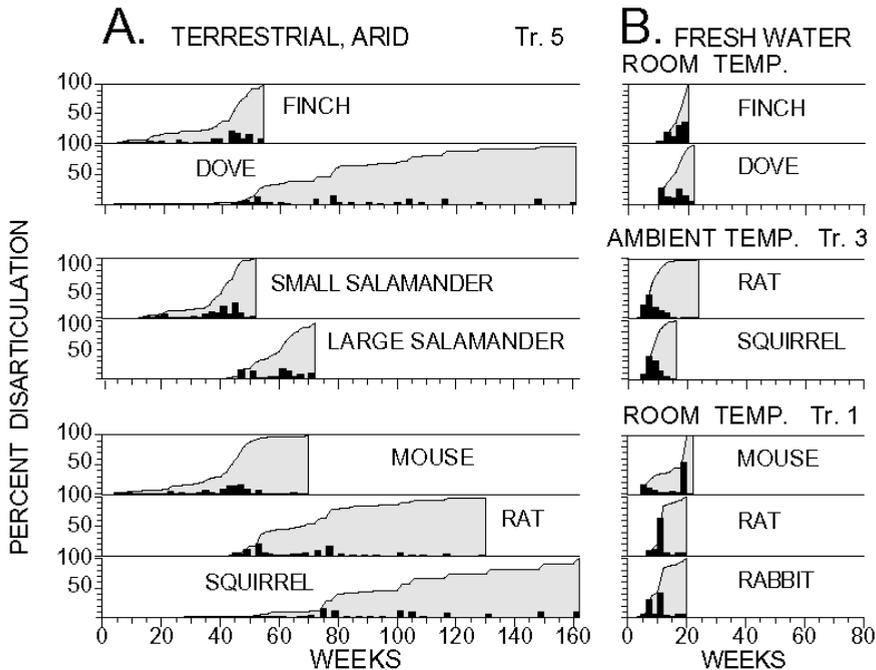


FIGURE 4. Comparison of mean disarticulation times for different size categories of carcasses, in several treatments. See Figure 3 for explanation of graphs.

times in freshwater (Figure 4B; Table 5E). In the wet cage (high rainfall, Tr. 6) there also were no significant differences between species (size classes) in disarticulation time (Table 5F). Disarticulation times for the two species of lizard in Trs. 3 and 5 did not differ significantly (Table 5C), so data from the two species were combined in all analyses.

Rainfall had a significant impact on disarticulation in the dry terrestrial environment (Tr. 5). Most disarticulation of small salamanders, lizards, finches, and mice occurred during the rainy season near the end of the first year of the experiments (Figures 2, 3, 4a). Disarticulation began much earlier than this, but the rainy season greatly accelerated the process.

Disarticulation of large salamanders, doves, rats, and squirrels began during the rains near the end of the first year (Figures 3, 4A), but disarticulation rates thereafter did not seem to be related to rainfall.

Disarticulation Sequence

Figures 5-9 show sequences of disarticulation in the larger species of each class. Analysis of the disarticulation sequence for individual carcasses was attempted but did not provide information beyond the disarticulation graphs. The graph medians show average disarticulation sequences, but there is variability in the sequence at the individual level. For

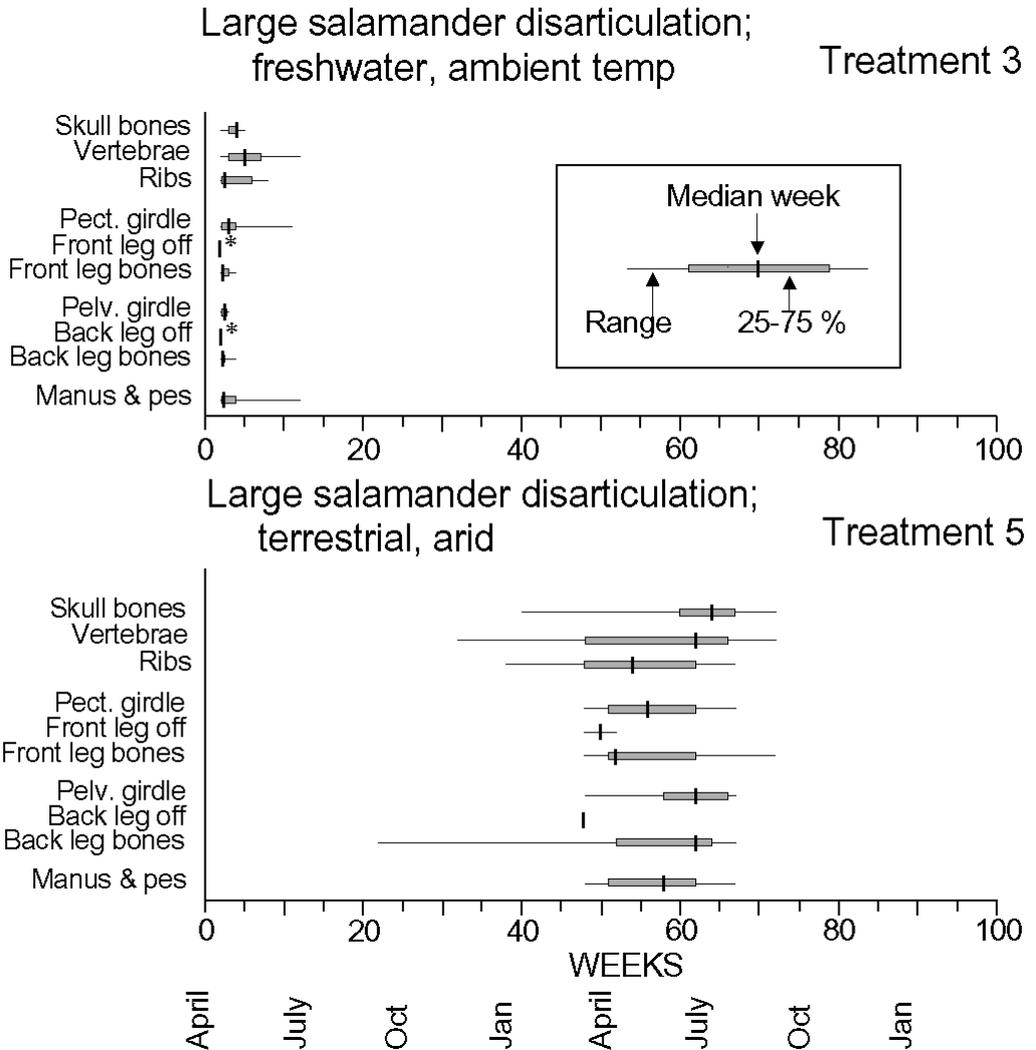


FIGURE 5. Disarticulation sequence for large salamanders in Trs. 3 and 5. Based on all disarticulation events, which includes separation of individual bones from body, and also separation of larger body parts (entire leg, e.g.) from the body. Graphs show week of median disarticulation event for each category, quartiles (week in which 25% and 75% of disarticulation events had occurred), and ranges. In Tr. 3, some grouping of bones was done, because of the small variance between bones. * indicates small sample for separation of limb from body, because often the limb was held to the body by skin, while individual limb bones disarticulated. ** indicates that some bones were still articulated when the experiment was ended after 3 years.

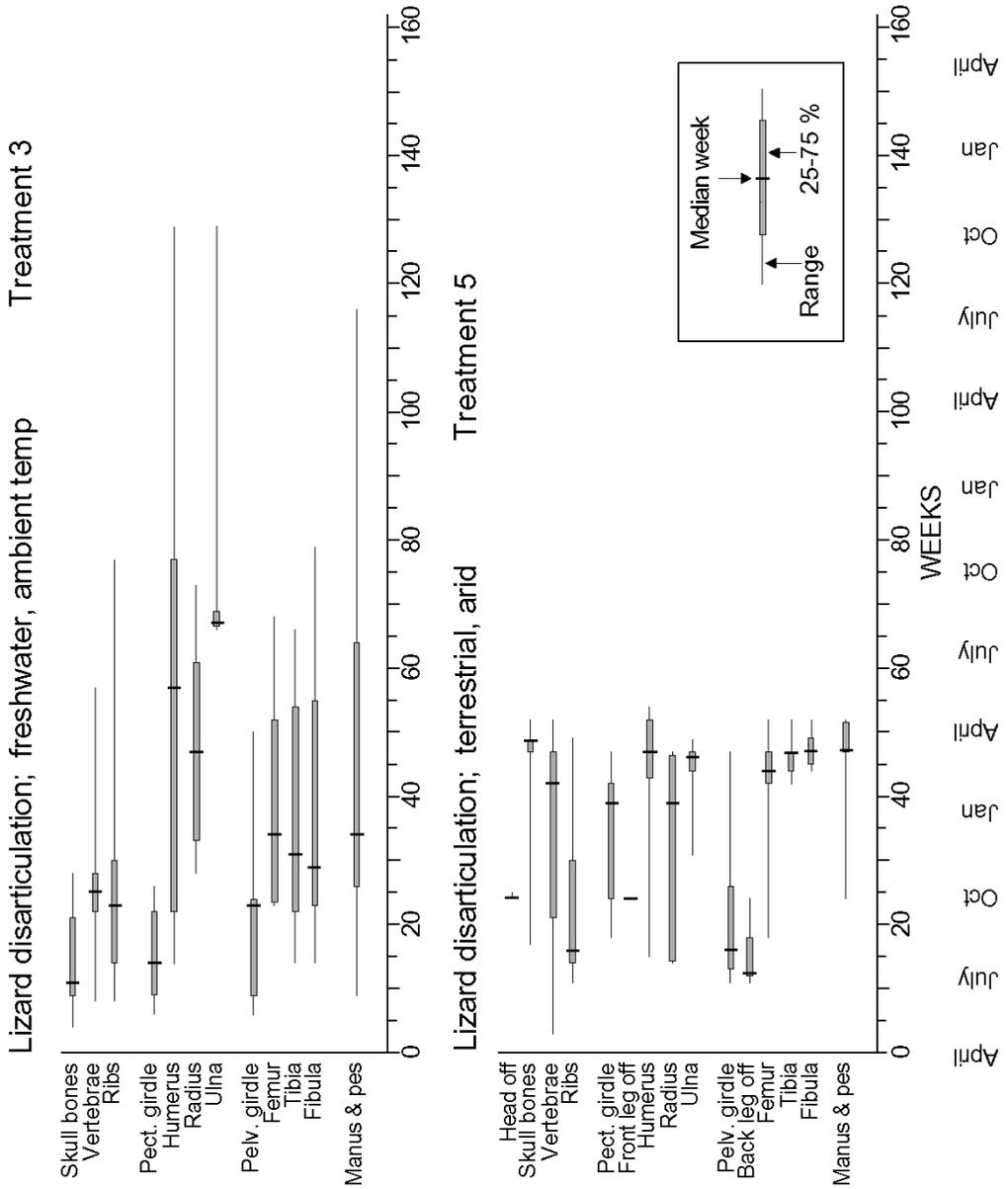


FIGURE 6. Disarticulation sequence for lizards in Trs. 3 and 5. See Figure 5 for explanation of graph.

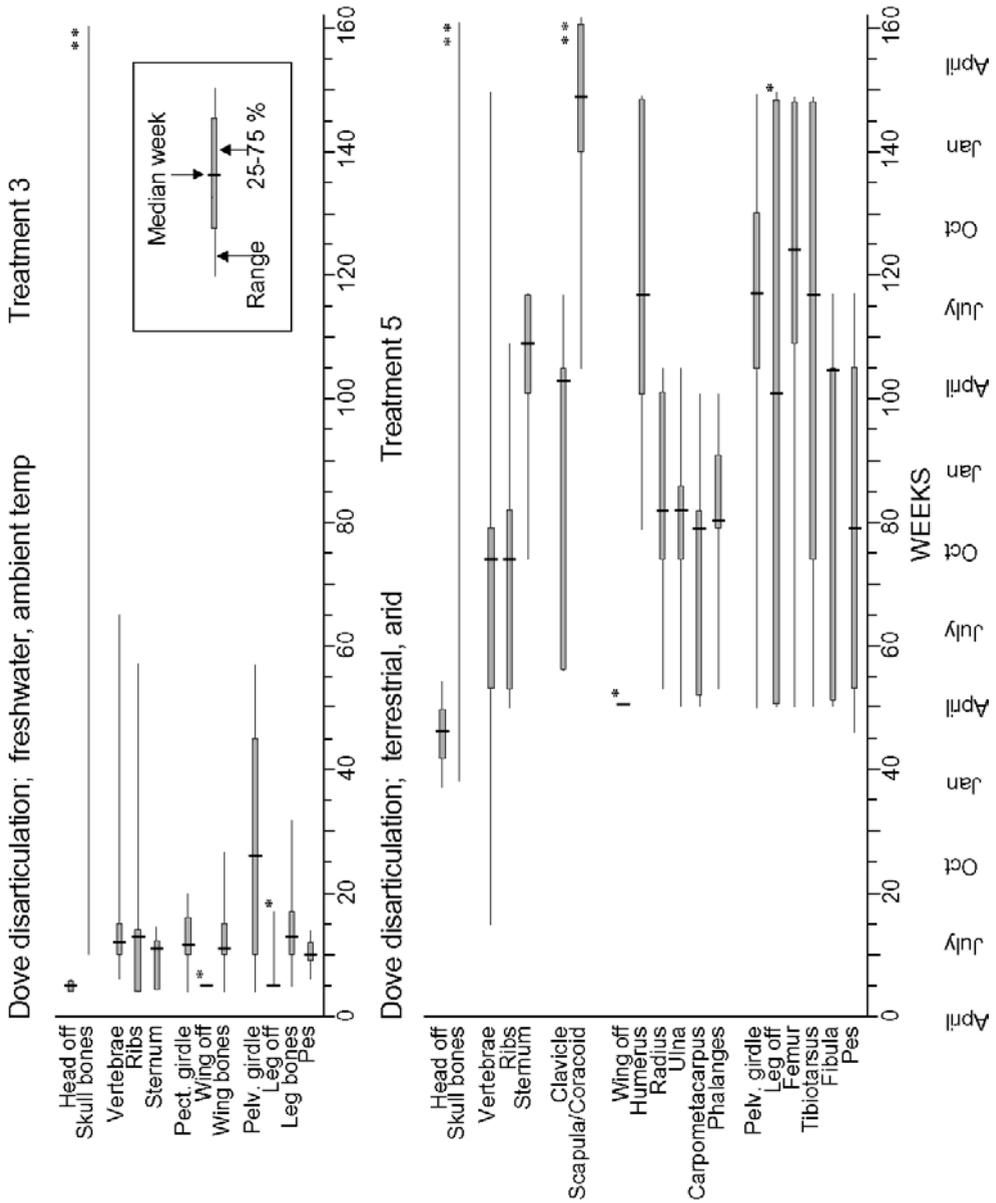


FIGURE 7. Disarticulation sequence for doves in Trs. 3 and 5. See Figure 5 for explanation of graph.

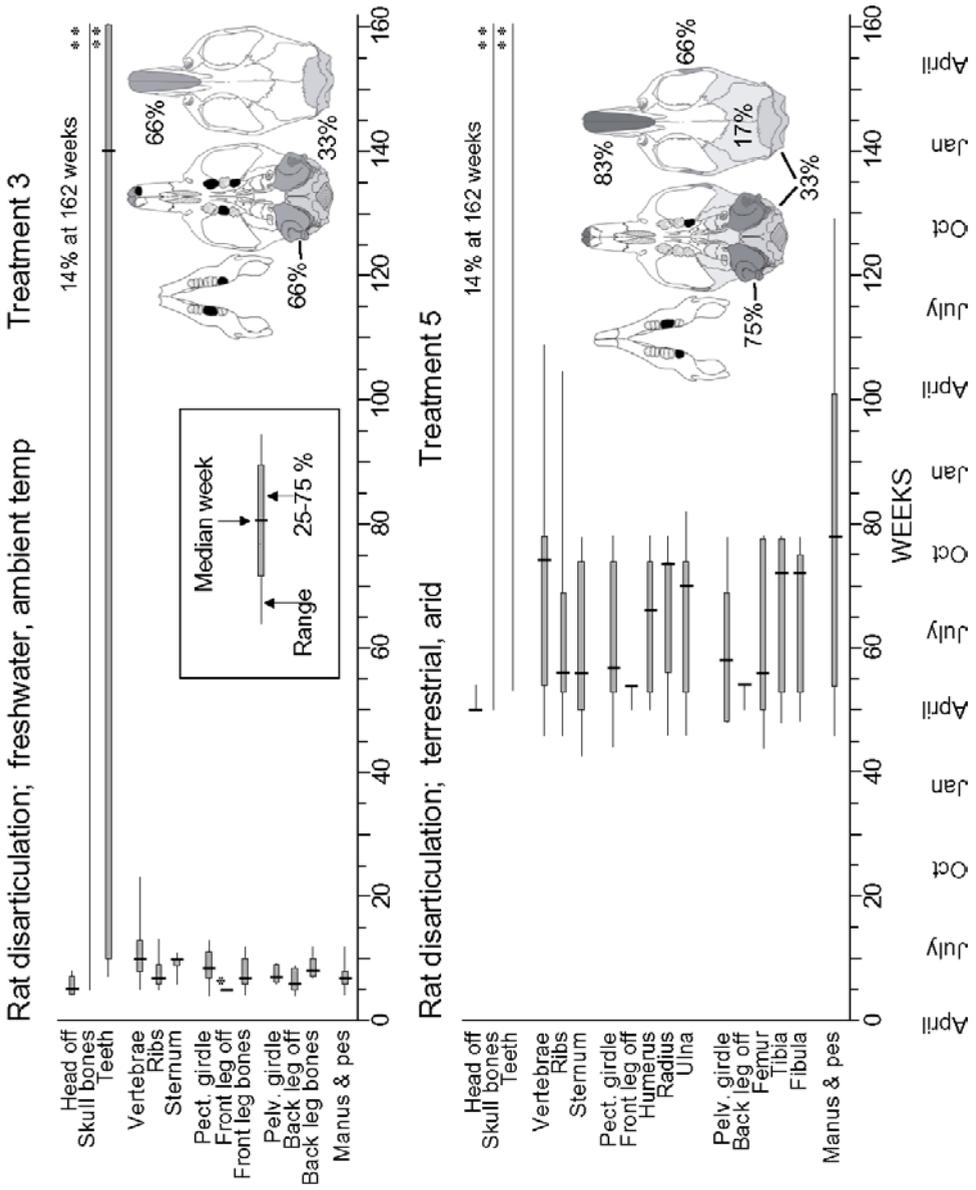


FIGURE 8. Disarticulation sequence for rats in Trs. 3 and 5. See Figure 5 for explanation of graph. Skull diagrams show average number and type of teeth lost from skull by the end of three years (black spaces or missing lower incisors), and shaded bones show percent of each bone type separated, on average, from skull by the end of three years.

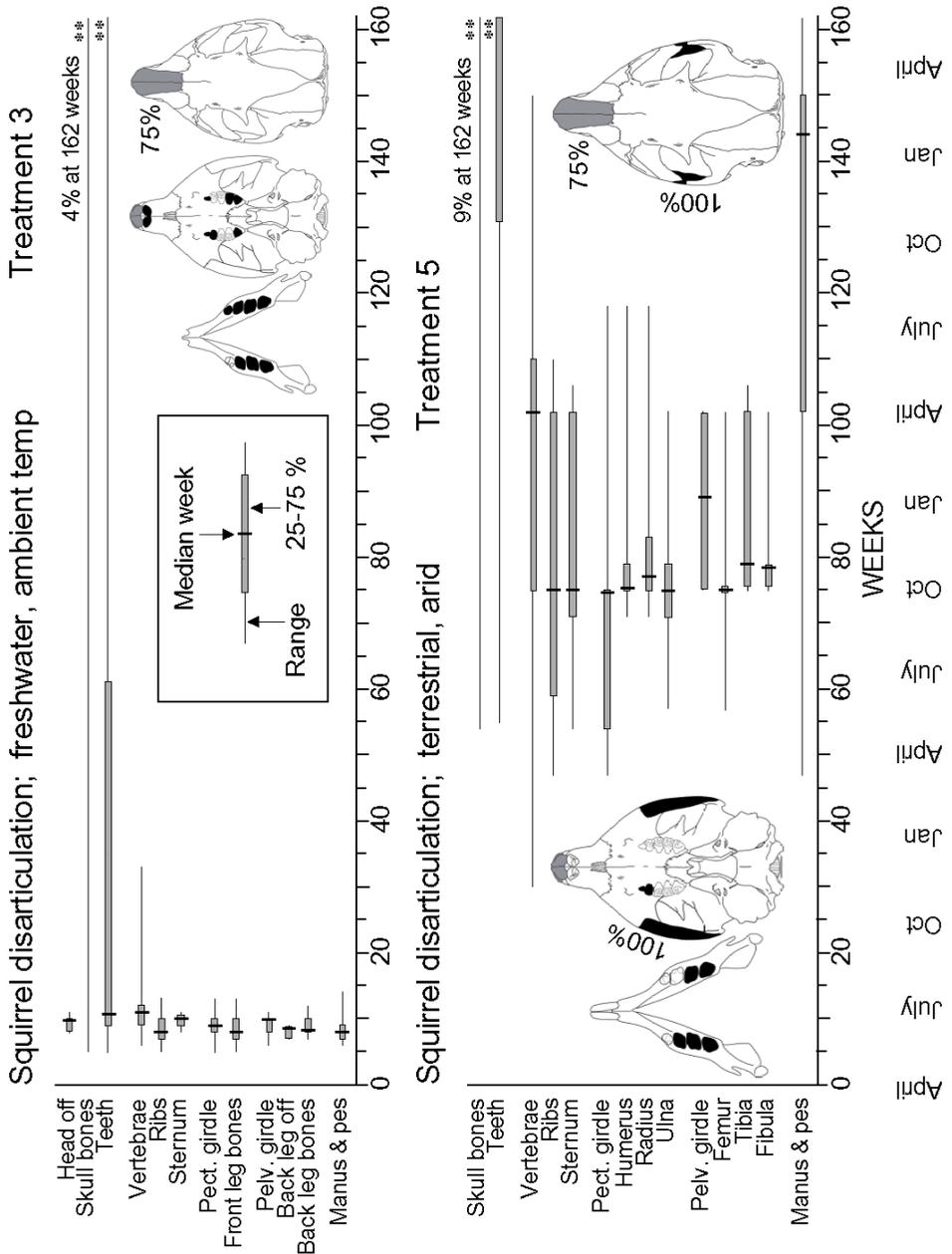


FIGURE 9. Disarticulation sequence for squirrels in Trs. 3 and 5. See Figures 5 and 8 for explanation of graph.

Table 6. Statistical tests for concordance of disarticulation sequences, tested with Kendall's coefficient of concordance (W).

Concordant sequences: no significant differences in disarticulation sequences

1. Disarticulation sequences measured at median, 25%, and 75% disarticulation between Trs. 3 and 5 for large salamander, lizard, dove, rat, and squirrel (species tested separately and pooled) ($W = .463-.639$; chi square = 20.19-78.80; $df = 7$; $p < .005$).
2. Median disarticulation sequences of finches and doves in all treatments (tested separately and pooled) ($W = .347-.697$; chi square = 14.20-19.42; $df = 7$; $p < .01-.05$).
3. Median disarticulation sequences of rats and squirrels in all treatments (tested separately and pooled) ($W = .374-.487$; chi square = 12.83-23.57; $df = 7$; $p < .005-.05$).

Discordant sequences: disarticulation sequences different between groups

1. Large salamanders and lizards were not significantly concordant in their median disarticulation sequences, for all treatments (salamanders alone: $W = .142$; chi square = 4.97; $df = 7$; $p > .5$. Lizards alone: $W = .319$; chi square = 11.15; $df = 7$; $.25 > p > .10$. Salamanders and lizards together: $W = .193$; chi square = 13.49; $df = 7$; $.10 > p > .05$).
-

example, in terrestrial rats the skull usually came off first, but in one case it was late in the process.

The graphs often show individual limb bones disarticulating after the limb has separated from the body. This is because a separated body part containing more than one bone (e.g. a lower leg) was left in place until all bones in that body part separated from each other. Their individual bones were collected as they separated from the body part.

In salamanders, lizards, birds, and rats, on average, legs separated from the body before separation of most of the individual bones of the body and long bones of the limbs (Figures 5-8). In other respects the sequence was more variable. In some groups there were low sample sizes for limbs separating from the body, because skin held the limb attached to the body while individual limb bones came off. For

most species and treatments there were no significant differences in disarticulation sequence (Table 6). Salamanders and lizards were the exception, and the greatest variation between salamanders and lizards was in the timing of disarticulation of skull bones and pectoral girdle.

There was wide variability in disarticulation time of vertebrae. Some vertebrae came loose early in the disarticulation sequence, but clusters of vertebrae remained attached together late in the process. A similar effect occurred in the disarticulation of the manus and pes. The widest variability in the disarticulation process was seen in terrestrial environments for most groups, and in freshwater lizards.

Disarticulation of skulls and teeth

When salamanders began to disarticulate,

Table 7. Timing of loss of teeth by mammals in taphonomy experiments, showing number of weeks to first tooth loss, loss of 25 percent of teeth, median tooth loss, and 75 percent tooth loss.

Species	N	Time in Weeks				% lost in 3 years
		1st. tooth loss	25%	Median	75%	
Freshwater, ambient temperature		Treatment 3				
Rat	4	7	15	140	---	53
Squirrel	4	5	9	11	61	82
Terrestrial		Treatment 5				
Mouse	6	65	—	—	—	21
Rat	6	53	—	—	---	11
Squirrel	3	55	131	—	---	35
Terrestrial, high rainfall		Treatment 6				
Mouse	2	37	—	---	---	8
Rat 2	27	36	—	---	35	
Squirrel	1	15	30	---	---	45
Terrestrial, then freshwater		Treatment 7				
Rat	2	10	16	86	---	69
Squirrel	1	12	14	24	---	73

Percent of teeth lost by three years (rats + squirrels only): (CT = cheek teeth)

	<u>Freshwater (Tr. 3 + 7)</u>	<u>Terrestrial (Tr. 5 + 6)</u>
Upper CT	70% lost	16% lost
Lower CT	65%	49%
Incisors	73%	2%

their skulls quickly fell apart into their constituent bones. Lizard skulls were more durable, but eventually fell apart. In contrast, mammal and bird skulls separated from the body early in the process, but were resistant to further disarticulation. At the end of the three year experiment all mammal skulls were at least partially intact

(Figures 8, 9). Under most conditions teeth began to come out of mammal skulls within 7-13 weeks (Table 7), but many teeth were still present after 3 years. Squirrels lost more teeth than mice or rats, and tooth loss was much greater in water (Tr. 3 and 7) than for terrestrial specimens (Tr. 5 and 6). Terrestrial specimens of rats and squirrels

(Tr. 5 and 6) lost significantly more lower cheek teeth than upper cheek teeth (49% vs 16%) (Mann Whitney test; $U = 1$; $p < .05$) (Table 7). Bird skulls are mostly fused bones, and only a few small bones separated from the skull, including the beaks from 25% of freshwater doves and most beaks of terrestrial finches and doves.

Because of the differences in the skull disarticulation process, skulls of different taxa were treated differently in Figures 3 and 4. Since salamander and lizard skulls disarticulated as fast or faster than the rest of the skeleton, their skull bones were included with the rest of the data for these carcasses. Bird and mammal skulls, however, remained largely intact throughout the experimental period, and are not included in the data presented in Figs. 3 and 4. If the skulls had been included, it would have appeared that birds and mammals took the entire three years to disarticulate under all experimental conditions, which would be misleading. At the end of the three years the only skeletal elements other than bird and mammal skulls still articulated were two dove scapula/coracoid units (Figure 7).

Weathering

Most bones were not exposed to the weather for long periods after the flesh covering the skeleton was gone. The primary exceptions were mammal and bird skulls that remained in the experimental chambers throughout the three year study. No weathering of bones was detected under these experimental conditions.

Rat and squirrel teeth in the terrestrial treatments contained a number of

small cracks by the end of three years (Table 8). These cracks were present in teeth that were transferred to water (Tr. 7) or to the wet cage (Tr. 6), as well as those that remained in the dry terrestrial setting. The first cracks in incisors were longitudinal to the tooth, generally beginning on the inside surface and/or front surface and then extending all the way through the tooth. Cracks on the cheek teeth began by cracking across the occlusal surface and then extending into the tooth. In contrast, no cracking was observed in teeth that were in freshwater or seawater for three years. Some rat incisors in the dry terrestrial treatment were broken off at or near their point of emergence from the jaw, but this was not seen in squirrels. Mice teeth had the smallest incidence of cracks and breaks.

Discussion

This study of decay and disarticulation in small modern vertebrates under controlled conditions allows direct comparison of results across several environments and across taxa and size classes, broadening the background against which fossil assemblages can be interpreted. Bacterial decay of carcasses in water occurs within a few months, contrasted with rapid removal of soft tissues by insect larvae in a terrestrial setting, followed by slow disarticulation of the dried carcass. The rate and sequence of the disarticulation process varied with carcass size and the nature of the animal's skin.

In some cases disarticulated bones were found that seem to have been hidden under debris for an unknown time, with

Table 8. Cracks and breaks present in mammal teeth at the end of the three-year experiment, in Tr. 3 (freshwater), Tr. 4 (seawater), Tr. 5 (terrestrial), Tr. 6 (terrestrial wet), and Tr. 7 (terrestrial followed by freshwater) given in mean number of cracks or breaks per tooth. Cheek teeth (CT) = premolars + molars (squirrels have two upper and one lower premolar, and three molars in each jaw. All others have three molars in each jaw and no premolars).

Treatment	N		Cracks		Breaks		Cracks + breaks/tooth
	Incisors	CT	Incisors	CT	Incisors	CT	Incisors+CT
3-rats	5	24	0	0	0	0	0
3-squirrels	0	14	0	0	0	0	0
4-rats	13	36	0	0	0	0	0
5-mice	17	36	2	2	2	0	0.11
5-rats	22	60	18	44	5	0	0.93
5-squirrels	10	34	18	27	0	0	1.02
6-mice	6	15	1	0	0	0	0.05
6-rats	7	14	5	5	2	0	0.57
6-squirrels	4	8	1	5	0	0	0.50
7-rats	2	7	0	0	1	0	0.11
7-squirrels	2	5	2	2	0	0	0.57

some smaller bones temporarily buried in earthworm holes. It is not likely that this occurred often enough to have a significant affect on the results, but some median disarticulation times reported here are probably slightly longer than they should be.

Disarticulation times are maximums; under natural conditions the influence of predators and scavengers will likely produce shorter disarticulation times (Mellett 1974; Dodson and Wexlar 1979; Andrews and Evans 1983; Behrensmeyer 1991; Allison and Briggs 1991), and in some circumstances disarticulation can occur in minutes after death (Behrensmeyer 1991). Some may argue that our experiments are not relevant to the

interpretation of fossils because of the absence of scavengers (larger than insects) and carnivores. However, the purpose of an experimental study under controlled conditions is to isolate and determine the effects of each significant variable that will affect the taphonomic process. Comparative, controlled studies supplemented by field observations in natural conditions will yield the most complete understanding of the overall process and how it differs under different conditions. As stated by Briggs (1995, p. 540), “only by simplifying conditions and exploring the effect of changing variables can we investigate the most important factors that influence fossilization, and determine their role.”

In terrestrial systems saprophagous insects and microbes remove soft-tissues one to two orders of magnitude faster than microbes alone (Payne 1965; Allison and Briggs 1991). We observed this in the rapid removal of soft-tissues prior to desiccation of carcasses in the terrestrial conditions, in contrast to the much slower process of tissue decay in water. The preserving effects of desiccation in a completely dry environment (Weigelt 1989; Behrensmeyer 1991) was evident in our experiments, and rain was an important factor in reactivating decay and disarticulation, affecting smaller carcasses more than larger species.

Disarticulation was most rapid for carcasses in water, since the tissues holding bone joints together apparently decay at about the same rate as other tissues. Most experimental species completely disarticulated within six months (Figures 3, 4). In contrast, dry rat-sized carcasses could remain articulated for a year or more in a terrestrial environment if not damaged by scavengers (Figures 3, 4), since insect larvae did not completely destroy the skin or ligaments across joints.

The long flotation times typical of birds and mammals in water can reduce the chances of fossilization of complete skeletons. Bones dropping from floating carcasses can be spread over a large area (Schäfer 1972). Two important factors present in natural settings that were not replicated in these experiments are the action of wind and water currents. Carcasses floating in water are likely to be moved by wind and/or flowing water and deposited on shore, where they would be subject to scavenging and other terrestrial influences, perhaps becoming part of a microvertebrate accumulation (Mellett

1974; Dodson and Wexlar 1979). In a natural environment, aquatic scavengers would also have access to floating carcasses, and could alter the taphonomic process. On the other hand, floating carcasses could be concentrated on shore and covered by flash flood deposits as a mass mortality assemblage. These processes can be important, since a significant part of the terrestrial vertebrate fossil record occurs within fluvial deposits (Behrensmeyer 1988).

Transferring carcasses from the dry ground surface into water in Tr. 7 may be analogous to a natural process common in some environments: the movement of carcasses from a terrestrial to a fluvial or lacustrine system by flash floods or runoff. For carcasses not consumed by predators or scavengers, this process has the potential to produce the most rapid disarticulation regime. This regime is unlikely to result in complete fossil skeletons, unless the flowing water that transports them also buries them within a few days.

These data give upper limits for interpretations of time from death to burial of fossil assemblages. If the depositional environment is known, the presence of articulated small vertebrates can provide more temporal resolution for depositional rates than is likely to be provided by sedimentological data alone. A study of Eocene turtles and associated sediments illustrates the benefits of combined study of taphonomy and sedimentology to determine the depositional regime (Brand et al. 2000; Buchheim et al. 2000). A fossil assemblage containing articulated or partially articulated small vertebrates was likely buried within a few months after death of the articulated individuals if they were in water, or within a

few years in a dry terrestrial environment. This time is dependent on animal size in dry terrestrial environments, but independent of size in water. Longer times after death would result in more disarticulation.

Amphibians and reptiles

The tendency of lizard skin to hold together as a strong but limp bag with bones inside could cause misinterpretation of some fossils. If some extinct reptiles had the same type of skin, their articulated fossil limbs or other body portions could be interpreted as evidence of rapid burial, although the animals may have been dead for a considerable time before burial, with their limb bones held together by the skin, in water. Carcasses of some large marine mammals drift for weeks, while bones dropping from this drifting sack are spread over miles of sea floor (Schäfer 1972). This process could also occur on a smaller scale with lizards, as some bones fall out of the skin bag while it floats in the water currents. Even though the type of skin will be unknown for extinct animals, it is still helpful to be aware of the effect of this variable, and the range of interpretations of fossils that it may allow.

Mammals and birds

Comparing disarticulation sequence of doves in this study and in Bickart's (1984) study illustrates the magnitude of variation that can occur in these sequences, from differences in species or in experimental conditions. In Bickart's study rock dove sternums came off early. In our

study they came off early in water but late in terrestrial conditions. Bickart's doves' legs disarticulated before wings, but in our study it was the opposite (Figure 7). Oliver and Graham (1994) suggest that the early loss of some leg joints in Bickart's doves may have been due to rodent scavenging. In Bickart's study the proximal wing joints disarticulated before the distal wing joints, but in our study the trend was partially reversed. In both studies the pectoral girdle disarticulated late.

Davis and Briggs (1998) studied a variety of bird carcasses in a brackish swamp and marine embayment in Florida, where temperatures averaged 5-10 degrees C warmer than in our experiments. Specimens that were protected from scavenging decayed and disarticulated within 4-10 weeks, faster than in our experiments. The basic disarticulation sequence of protected specimens was similar to our results with doves (Figure 7). Skulls detached first, and then the limbs separated from the body before the individual limb bones disarticulated.

There were some similar trends in disarticulation sequence between our results and field studies of much larger mammals. Hill (1979) concluded from his and other studies that in bovids "it looks as though the presence of external water leads to disarticulation from the extremities, whereas limbs disarticulate more or less proximally to distally in drier conditions." With the much smaller mammals in our study, there is some tendency for this same pattern to occur with rats and squirrels (Figs. 8, 9). The process occurred too rapidly in water to draw definite conclusions. Hill and Behrensmeyer (1984) found that skulls and limbs of African

savannah mammals tend to come off the skeleton first, and then limbs disarticulate into their individual bones. The small mammals in our study followed the same pattern.

In our experiments there was a large range of variation in disarticulation time for most bone types, within any given taxon. This variation, along with the variation in disarticulation sequences described above, emphasizes the need for caution in interpreting the history of articulated joint frequencies in fossil vertebrates, without a substantial body of data on disarticulation of the specific taxa being studied, under various conditions. Taphonomic conclusions based on averages from a large fossil sample will be most meaningful. A few examples of unexpected fossil disarticulation patterns may just reflect the wide range of variation in taphonomic processes, and will not be a reliable basis for general conclusions.

Disarticulation sequences in small vertebrates do not seem to provide useful data for inferring the environment of a fossil assemblage during the disarticulation process, because of the variability in disarticulation sequences and lack of significant differences between experimental environments.

Mammal and reptile teeth and jaws

In our experiments loss of teeth by rats and squirrels increased with increasing body size, and with increase in presence of water in the environment (Table 7). Mice lost fewer teeth than this trend would have predicted. Cracking of rodent teeth was absent if they were always in water, but was

common in terrestrial environments, and also in rodents placed in water or the wet cage after 53 days in dry terrestrial conditions. This indicates that the cracking process began before day 53, and was not reversed by subsequent wet conditions or submergence. It is not known whether early burial would alter this process.

A fossil assemblage containing numerous rodent jaws with most teeth present and intact presents certain constraints on its interpretation. In our study, rodent jaws retained more teeth in a dry environment, but cracking was common as long as teeth were in dry conditions for about the first two months (Table 8). Cracking did not occur in water, but more teeth were lost in water. Thus a fossil assemblage of rodent jaws with all or most teeth, with no cracks, suggests continuous submergence in water and fairly rapid burial, before tooth loss. Conditions in this study produced skulls with teeth, but not maxillary bones with teeth, separated from the rest of the skull. Further work is needed on the effects of owls, raptors, or other influences that may separate small mammal maxillaries from skulls.

Rat- to squirrel-sized mammals lost significantly more lower cheek teeth than upper cheek teeth in terrestrial conditions, but there was no significant difference in water. This factor could provide a clue to original paleoenvironment of deposition of a fossil assemblage, but more experiments are needed with a wider variety of species and sizes of mammals.

Isolated intact fossil mammal teeth with no cracks are most likely the result of disarticulation in water, with its high tooth loss and absence of cracking. Lizard teeth were almost never lost in our experiments,

in contrast to the common tooth loss in mammals. More experiments with a variety of reptile jaws are needed to determine the conditions under which reptiles lose teeth in the disarticulation process.

Some aspects of our data, such as the affects of different types of skin, underscore the need for actualistic study of a greater diversity of organisms to provide a more complete framework for understanding taphonomy of fossil animals. The explanation of some of the unobservable fossilization events in the ancient past will always be uncertain, but real-world data like those reported here can reduce the level of uncertainty.

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REFERENCES

- Allison, P. A. and Briggs, D. E. G. (1991). Taphonomy of nonmineralized tissues. In Allison, P. A. and Briggs, D. E. G., eds. *Taphonomy: Releasing the Data Locked in the Fossil Record*. Topics in Geobiology, vol. 9. Plenum, New York, pp. 25-70.
- Andrews, P. and Nesbit Evans, E. M. (1983). Small mammal bone accumulations produced by mammalian carnivores. *Paleobiology*, 9:289-307.
- Barnes, R. S. K. and Mann, K. H., eds. (1991). *Fundamentals of Aquatic Ecology*, 2nd ed. Blackwell Scientific, Oxford.
- Behrensmeyer, A. K. (1988). Vertebrate preservation in fluvial channels. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 63:183-199.
- Behrensmeyer, A. K. (1991). Terrestrial vertebrate accumulations. In Allison, P. A. and Briggs, D. E. G., eds. *Taphonomy: Releasing the Data Locked in the Fossil Record*. Topics in Geobiology, vol. 9. Plenum, New York, pp. 291-335.
- Bickart, K. J. (1984). A field experiment in avian taphonomy. *Journal of Vertebrate Paleontology*, 4:525-535.
- Brand, L. R., H. T. Goodwin, P. G. Ambrose, and H. P. Buchheim. 2000. Taphonomy of turtles in the Middle Eocene Bridger Formation, SW Wyoming. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 162:171-189.
- Briggs, D. E. G. (1995). Experimental taphonomy. *Palaaios*, 10:539-550.
- Buchheim, H. P., L. R. Brand, and H. T. Goodwin. 2000. Lacustrine to fluvial flood-plain deposition in the Eocene Bridger Formation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 162:191-209.
- Davis, P. G. and Briggs, D. E. G. (1998). The impact of decay and disarticulation on the preservation of fossil birds. *Palaaios*, 13:3-13.
- Dodson, P. (1973). The significance of small bones in paleoecological interpretation. *University of Wyoming Contributions to Geology*, 12:15-19.
- Dodson P. and Wexlar, D. (1979). Taphonomic investigations of owl pellets. *Paleobiology*, 5:275-284.
- Hill, A. (1979). Disarticulation and scattering of mammal skeletons. *Paleobiology*, 5:261-274.
- Hill, A. and Behrensmeyer, A. K. (1984). Disarticulation patterns of some modern East African mammals. *Paleobiology*, 10:366-376.
- Mellet, J. S. (1974). Scatological origin of microvertebrate fossil accumulations. *Science*, 185:349-350.
- Norusis, M. J. (2000). *SPSS 10.0 Guide to Data Analysis*. Prentice Hall, Upper Saddle River, New Jersey.
- Nunn, C. L. and Smith, K. K. (1998). Statistical analyses of developmental sequences: the craniofacial region in marsupial and placental mammals. *The American Naturalist*, 152:82-101.
- Oliver, J. S. and Graham, R. W. (1994). A catastrophic kill of ice-trapped coots: time-averaged versus scavenger-specific disarticulation

- patterns. *Paleobiology*, 20:229-244.
- Payne, J. A. (1965). Summer carrion study of the baby pig *Sus scrofa*. *Ecology*, 46:592-602.
- Schäfer, W. (1972). *Ecology and Palaeoecology of Marine Environments*. The University of Chicago Press, Chicago.
- Toots, H. (1965). Sequence of disarticulation in mammalian skeletons. *University of Wyoming Contributions to Geology*, 4:37-39.
- Weigelt, J. (1989). *Recent Vertebrate Carcasses and Their Paleobiological Implications*. University of Chicago Press, Chicago. (English translation from the German original, published in 1927)
- Zar, J. H. (1984). *Biostatistical Analysis*. 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

