

PRESERVATION OF SPECIES DIVERSITY AND ABUNDANCES IN PACIFIC ISLAND LAND SNAIL DEATH ASSEMBLAGES

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Abstract Data from 11 land snail surveys undertaken on the islands of the Pacific (Hawaii, American Samoa, Palau) are analyzed in order to ascertain the proportions of species represented in the death assemblage alone or the live assemblage alone, and whether the abundances of the individual species in the two assemblages are correlated. The percentage of species collected only as dead shells ranged from 13 % to 52 % (mean = 31.6 %), while that found only in the live assemblage was considerably lower (mean = 10.2 %). At nine of the 11 localities the rank abundances of species in the dead and live assemblages were significantly correlated, although in most cases the correlation was not strong. Taphonomic differences among species and localities as well as sample sizes may weaken the correlations, but real change in abundances of certain species may also be involved.

Key words Mollusca, land snails, Pacific islands, biodiversity, taphonomy.

INTRODUCTION

Pacific island land snail faunas are among the most diverse in the world, in terms of both species richness and ecological and morphological diversity (e.g. Cowie, 1996a, b). Huge evolutionary radiations of endemic species have attracted the attention of biologists for many years (e.g. Garrett, 1884; Gulick, 1905; Pilsbry & Cooke, 1912-1914; Solem, 1983; Cowie *et al.*, 1995a; Cowie 1998a). These faunas, however, are highly threatened by human-mediated changes in their environment, including habitat destruction and the introduction of alien species (including snail predators introduced for biological control), and have probably suffered as a result of over-collecting (Hadfield, 1986; Hadfield *et al.*, 1993; Cowie, 1992; Cowie & Cook, 2001; Cowie & Robinson, 2003). Their evolutionary uniqueness and precarious conservation status make them potentially important subjects for research in both evolutionary and conservation biology.

Land snail diversity surveys are the most fundamental part of such research, particularly because many Pacific island land snail faunas are still poorly known (Cowie 1996a; Cowie & Rundell, 2002; Cowie *et al.*, 2002). Surveys are vital to future conservation management, as they constitute the baseline from which to track changes in species distribution and abundance, including extinctions.

Live-dead assemblage agreement studies, which investigate whether the relative abundances present in the live assemblage are reflected in the death assemblage, have been an important means of assessing whether researchers can rely on information gathered from only the death assemblage, such as that gathered from the fossil record (Johnson, 1965; Kidwell, 2001a). Recent studies of marine invertebrate assemblages have shown that in some cases, but not all, there is high fidelity between life and death assemblage abundances (Kidwell 2001a, b; Warwick & Light, 2002).

It is widely accepted that tropical terrestrial faunas do not preserve well and are seldom represented in the fossil record, perhaps because of the often acidic rainforest soils and the consequent rapid decomposition (Tappen, 1994). Dry forest death assemblages may also be subject to the harsh weathering forces of wind and temperature and moisture

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fluctuations (Behrensmeyer, 1978). However, land snail fossils and "subfossils" (old-looking shells often of unknown age) are often found on Pacific islands in large accumulations (Cooke & Kondo, 1952; Christensen & Kirch, 1981, 1986, Dixon *et al.*, 1997), indicating that some species' shells can indeed be preserved for extended periods. Furthermore, dead shells are always encountered and often collected along with live snails during surveys and are assumed to provide information on current and past species' distributions and abundances. Unlike many terrestrial invertebrates, land snails often leave behind significant, identifiable (generally to species-level) traces of their existence (their shells) for many years, making them potentially important indicators of invertebrate community change.

In this study, using 11 live-dead land snail datasets derived from surveys undertaken in Hawaii, American Samoa and Palau, we assess the following.

1) How much of the total species diversity at each site is present only in the death assemblage? If a species is recorded only in the death assemblage, it may be too rare to have been recorded in the live collections or may be locally extinct (both have ecological and/or conservation implications) (e.g. Preece, 1995, 1998; Bouchet & Abdou, 2001). The reverse may also be true, that some species are only collected as live specimens.

2) How well do relative abundances between live and dead collections match at each site? In areas where live snails are no longer present, it may be important to assess the relative abundances of the species that once existed there, as indicated by the death assemblage. Within areas that do still have live snails, changes in relative abundances among species are important from both ecological and conservation perspectives (e.g. Christensen & Kirch, 1986), and examination of the death assemblage may be a good way to deduce these changes.

3) How well do rank abundances in recently dead and long dead assemblages agree? Although it is difficult to assess how long a dead shell has been present on the ground, comparisons between more recently dead-looking shells (with periostracum and pigmentation intact) and long dead-looking shells (no periostracum, bleached white, possibly cracked) may show that either changes in community composition were quite recent (if dead and long dead assemblages agree more than live-dead assemblages in rank order abundances), or at least that species do not drop out of the potentially fossilizable shell assemblage right away, and species abundances are captured even in the long dead assemblage.

METHODS

Eleven datasets from a range of habitat types and islands (Table 1), derived from surveys that were undertaken between 1992 and 2001 and incorporated 455 sampling stations, were selected for analysis. The raw data are available in the reports cited in Table 1 and from the Bishop Museum (Honolulu) Malacology Collection database. Collection methodologies have been explained in detail by Cowie (2001a). Briefly, timed sampling in the field rather than collection of litter/soil samples was the approach adopted, since this is the most efficient way to obtain large numbers of samples and large geographic coverage (see Emberton *et al.*, 1996). Such a methodology under-samples smaller snails but this does not influence the present analysis because the same methodology was used in all the surveys.

Records were compiled from the survey reports, each consisting of survey station, species and the number of live and dead specimens collected (in some cases recently dead and long dead shells were distinguished). Slugs were omitted because, lacking a shell, they were not readily identified in the death assemblage. Total numbers of live

TABLE 1
Survey locations, number of sampling stations, habitat types and data sources.

Island	Survey locality	No. of stations	Habitat Type	Data Source
Hawaiian Islands				
Hawaii	Waiakea, South Hilo	82	rainforest	Cowie <i>et al.</i> , 1999a; Howarth <i>et al.</i> , 1999
Hawaii	Saddle Road	28	mostly dry forest	Evenhuis <i>et al.</i> , 1996
Hawaii	Pohakuloa Training Area	59	dry forest	Cowie & Nishida, 1993
Hawaii	North Kohala	16	wet, highly disturbed	Cowie <i>et al.</i> , 1999b
Oahu	Waahila Ridge	33	dry forest	Cowie <i>et al.</i> , 1999c, d
American Samoa				
Tutuila	National Park of American Samoa	112	rainforest	Cowie & Cook, 1999
Tau	entire island	51	wet, various	Cowie & Cook, 1999
Ofu	entire island	18	wet, various	Cowie & Cook, 1999
Olosega	entire island	14	wet, various	Cowie <i>et al.</i> , 2002, unpublished
Aunuu	entire island	10	wet, various	Cowie & Rundell, 2002, unpublished
Palau				
Babeldaob	entire island	32	wet, various	Cowie <i>et al.</i> , 1996

and dead individuals of each species were determined for each of the surveys, combining sampling stations within each survey because numbers of individuals at each station were too low to permit valid statistical analysis. Combining stations within surveys was legitimate because environments did not vary greatly among most stations within each of the survey localities and because taphonomic differences among the stations were not being assessed.

Percentages of land snail species found only in the live and dead assemblages in each survey were calculated. For each survey locality, species were ranked according to their abundances in the live assemblage, the dead assemblage, and the long dead assemblage. Spearman rank correlation coefficients (Glantz, 1992) were then calculated for the live vs. dead (including long dead) and dead vs. long dead abundances.

RESULTS

The species collected in each of the surveys are shown in Table 2 (at end of paper) (excluding slugs). Summary data are given in Table 3. The percentage of species collected only as dead shells ranged from 13 % (Waiakea, Hawaii) to 52 % (Ofu, American Samoa) (mean = 31.6 %). Dry forests (Saddle Road, Pohakuloa Training Area, Waahila Ridge) generally had the highest proportion of species represented only in the

TABLE 3

Summary data for each survey: total number of species; percentages of species found only in the dead and live assemblages; and number of specimens collected live, dead and long dead (long dead data only available for Saddle Road and Pohakuloa Training Area).

Survey locality	Total species	% dead only	% live only	Number of specimens		
				live	dead	long dead
Hawaiian Islands						
Hawaii: Waiakea, South Hilo	15	13	33	1073	509	—
Hawaii: Saddle Road	15	47	7	70	643	757
Hawaii: Pohakuloa Training Area	16	40	0	263	4458	7145
Hawaii: North Kohala	6	33	0	33	103	—
Oahu: Waahila Ridge	21	43	5	56	1040	—
American Samoa						
Tutuila: National Park	28	17	11	7168	1360	—
Tau	22	18	14	1356	562	—
Ofu	27	52	11	568	818	—
Olosega	21	29	10	340	344	—
Aunuu	15	27	7	272	141	—
Palau						
Babeldaob	27	26	15	115	234	—

death assemblage, while the two rainforest sites (Waiakea, Tutuila) had the fewest. In all but one case (Waiakea) the percentage of species found only in the live assemblage (mean = 10.2 %; excluding Waiakea, mean = 7.9 %) was considerably lower than that found only in the death assemblage (mean = 31.4 %; excluding Waiakea, mean = 33.2 %), but there was no clear trend related to habitat type.

At nine of the 11 localities the rank abundances of species in the live and dead assemblages were statistically significantly correlated (Table 4). They were not significantly correlated at North Kohala (Hawaiian Islands) and Ofu (American Samoa). At the two localities for which the death assemblage was broken down into dead and long dead shells, the rank abundances of species in the dead and long dead assemblages were also significantly correlated (Saddle Road, Hawaii, Spearman rank correlation coefficient $r_s = 0.815$, $p < 0.001$; Pohakuloa Training Area, Hawaii, $r_s = 0.938$, $p < 0.001$).

DISCUSSION

SPECIES DIVERSITY CAPTURED BY LIVE AND DEAD ASSEMBLAGES

A greater percentage of total species richness was discovered in the death assemblages than in the live assemblages. In two of the 11 surveys (Pohakuloa Training Area, North Kohala) all species were represented in the death assemblage. Nevertheless, for the most part, neither the death assemblage nor the live assemblage captured overall species richness. In the two dry forest surveys (Pohakuloa Training Area, Waahila ridge) the proportion of specimens collected dead was much larger than in the other surveys; live snails are simply harder to find in such habitats because they tend only to be active during times of increased humidity, at other times secreting themselves deep in crevices and other harder to sample microhabitats. A species' absence from the live assemblage may reflect its local extinction, although it is also possible that more prolonged survey effort, and perhaps litter and soil sampling, may have increased the proportion of species represented in the live assemblage at these localities, and this is probably true generally (Kidwell, 2001a). Local extinction may well be the case for *Palline* sp. cf. *notera* on Babelaob (Palau), as most charopids appear to have declined severely in the Pacific (Solem, 1983). It may also be the case for *Allopeas gracile* on Olosega (American Samoa). This species, introduced widely by Pacific islanders prior to exploration of the Pacific by westerners (Christensen & Kirch, 1981, 1986; Kirch, 1983), was once extremely abundant (Pilsbry, 1906-1907) but is now rarely found alive (Cowie, 2001a, b).

Presence only in the live assemblage is more difficult to explain. In the wettest habitats (most notably Waiakea) dead shells may break down more quickly than in very dry habitats such as Pohakuloa Training Area and Waahila Ridge, reducing the likelihood of their being recorded in the death assemblages. A significant proportion of species only found alive at some localities, or at least found in much greater abundance in the live assemblages, are tree snails (e.g., *Pleuropoma beryllina*, *Diastole schmeltziana*). Why their shells are not well represented in the death assemblages (sampled on the ground) is not clear, although at least in the case of *D. schmeltziana* its shell is thin and probably disintegrates rapidly after death.

Given limited resources for biodiversity surveys of this kind, collecting data from both the live and dead assemblages is the most pragmatic strategy for capturing total species diversity. It may be particularly important for detecting recently established alien species. For example, in two of the datasets (North Kohala, Saddle Road), *Euglandina rosea*, a voracious introduced predator of other snails, was collected only from the death assemblage, although it is almost certainly part of the live assemblage. Even if such species represent a small percentage of the overall species diversity, it is important to recognize their presence as early as possible, in order to adapt management practices to minimize their spread (Cowie, 1997). Although collecting both sets of data is necessary, keeping them separate is important for detecting possible local extinction (see above).

SPECIES RANK ORDER ABUNDANCE CORRELATIONS

In all but two localities, the rank order abundances of species in the live and dead assemblages were correlated. In general, therefore, the death assemblage reflects the species composition in the live assemblage. This is important because at most localities a proportion of the species was missing from the live assemblage, especially in dry forest localities (see above). We can infer that probably these species that were absent in the sampled live assemblage were indeed present in the real live assemblage but were not found by the sampling methods adopted.

At two localities the rank order abundances in the live and death assemblages were not correlated. In one of these cases (North Kohala) this may be explained by the low number of species (six) and hence lack of statistical power. The other instance (Ofu) is

TABLE 4
Spearman rank correlations (r_s) between species abundances in the live and dead assemblages. p-values from Glantz (1992).

Survey locality	Number of species	r_s	p
Hawaiian Islands			
Hawaii: Waiakea, South Hilo	15	0.637	<0.02
Hawaii: North Kohala	6	0.653	n.s.
Hawaii: Pohakuloa Training Area	16	0.582	0.02
Hawaii: Saddle Road	15	0.559	<0.05
Oahu: Waahila Ridge	21	0.617	<0.005
American Samoa			
Tutuila: National Park	28	0.465	<0.02
Tau	22	0.508	<0.02
Ofu	27	0.210	n.s.
Olosega	21	0.466	<0.05
Aunuu	15	0.569	<0.05
Palau			
Babeldaob	27	0.427	<0.05

not easily explained.

However, although most localities exhibited a correlation between the live and death assemblages, in few cases was this a strong correlation. Many variables can influence a species being represented in both sampled assemblages, including different rates of breakdown of shells, different relative visibility (and hence likelihood of being sampled) in the live and death assemblages, rarity (resulting in sample sizes for some species being very small and the assemblage being dominated by a few very abundant species), and real changes in abundance over time.

We have no knowledge of relative rates of breakdown of different species' shells in different environments. We do not know how old the death assemblages are, nor the difference between the dead and long-dead assemblages in the two cases in which we have those data. Different species almost certainly degrade at different rates, and individual shells of a single species will also degrade at different rates depending on the microhabitat in which they find themselves (Carter, 1990). To take full advantage of land snail death assemblages for evolutionary and conservation studies, greater efforts to understand taphonomic processes must be made (cf. Bickart, 1984).

There may indeed have been real changes in community composition over time. Evidence from several species suggests that this might be the case (Cowie, 2001b). For example, in our study *Succinea konaensis* was collected at both Pohakuloa Training Area and Saddle Road (Hawaiian Islands), but out of 2343 specimens found, only 11 were alive. This species' historical range extends across most of the western side of the Island of Hawaii, an area of approximately 455 km² (Rundell, 2001). Although dead shells of *S. konaensis* are abundant throughout the historical range, it is difficult to find the species alive anywhere. Although some dry forest snails may have seasonal life histories resulting in their being active and readily found alive only at certain times of

year, this cannot account for this scarcity of live *S. konaensis* in the surveys because the larger survey at least (Pohakuloa Training Area) took place over six occasions spread throughout an entire year. It is possible that *S. konaensis* is suffering a real decline even in the small parts of its original wide range where it is still extant. If this kind of change is taking place in only one or a few species, then the overall correlation would be weakened but would not necessarily disappear.

CONCLUSION

With a better understanding of taphonomy, comparisons such as these could be used to analyze community change over time, which for most Pacific island land snail faunas has considerable conservation implications. Such studies are possible only for organisms that leave a substantial record of their presence after death, which among terrestrial invertebrates means essentially only the snails. Snails thus have the potential to be important indicators of relatively short term ecological change. Indeed, land snails already have been used to investigate change over a longer term archaeological time scale (Evans, 1972; Christensen & Kirch, 1981, 1986; David & Stanisic, 1991).

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