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Pitfall Traps Misrepresent the Terricoline Fauna in a Tropical Forest: A Novel Evaluation[2]

A critical evaluation of trapping efficiency in two rainforest biomes (primary vs. secondary forest) using a new combination of direct observation of events at widely used Barber pitfall traps, dry (= live) trapping, and the deployment of a trap funnel ensuring maximum retaining efficiency was conducted in the NW Panay Peninsula, Philippines. The omission of any preservative fluid ensured that neither attracting nor repelling odors confounded the results. The release of the live catch ensured that there was no depletion of local fauna and, hence, no 'digging-in' effect. Collectively, 12 traps, placed in identical linear arrays of six, in both types of forest each, yielded a total catch of 255 terricoline invertebrates (Oligochaeta, amphipod Crustacea, Myriapoda, Araneae, Insecta and their larvae). Two separate hours of direct observation per day of events of approach by terricolines to three of the traps in each habitat yielded a catch of a mere 21% of all individuals which made contact with a trap, or entered the outer funnel wall, but then turned away or exited and left. For the same reason, traps also failed qualitatively to portray the terricoline fauna by not trapping a formicine species of ant and an araneid spider. Hence, even with a maximum of precautionary naturalness, pitfall trapping grossly fails to reflect a terricoline community in terms of species abundance and composition.

INTRODUCTION

Barber pitfall traps, in short pitfall traps, are used widely by terrestrial ecologists and taxonomists. Deploying these traps provides insight into the species composition and species abundance of terricoline (= epigaeic) invertebrate taxa of an area (Southwood 1975, Steyskal & et al. 1986). The capture efficiency has been rarely assessed, in spite of its qualitative and quantitative importance. Among many situational factors, the presence and the nature of a preservative fluid, trap location, and trap dimensions and material

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have all been found to affect capture success, and, hence, portrayal of the fauna under study (Luff 1975, Seifert 1990, Weeks et al. 1997, Laeger & Schultz 2005). Additional confounding factors are the decline in capture numbers with time, the 'digging-in effect' (Greenslade 1973, Southwood 1975), and the behavior of potential trap victims—some ants managed to rescue themselves even after falling into the preservative, or used the trap as a dumping site for dead nest mates (Seifert 1990, Laeger & Schultz 2005). Aside from these significant observations, the behavior at and in the trap has received scant or no attention. What really happens at the trap has eluded most researchers who inferred distributional pattern from a faulty capture pattern.

Here we combine for the first time live pitfall trapping with direct observations at select traps and compare these data with the real captures at these and analogously placed traps nearby in two rainforest stands in the Philippines. The conclusions arrived at are particularly reliable since, unlike most research in field, the absence of a preservative has had neither a repelling nor an attracting effect. This has enabled us to suggest that pitfall traps portray the soil invertebrate fauna only to a very limited extent, and researchers are well advised to gauge capture efficiency by monitoring events around their traps, thereby replacing pattern-based conclusions with process-based conclusions. In addition, surveying the soil fauna in two differently disturbed habitats yielded some insight into the impoverishing effect of destruction and regrowth of primary forest. The significance of this aspect derives from the fact that the Philippines ranks number one globally in terms of biodiversity (Myers, et al. 2000) while registering a tremendous 82% destruction of its forests.

STUDY AREA AND METHOD

Pitfall trapping took place near Research Station 'Sibaliw' of the PESCP at the western border of a mosaic of primary and secondary (= second growth, 32 year old) rainforest of the NW Panay Peninsula (11°49'11.6'' N, 121°58'0.5''), 450 m asl, Philippines. Two equal sets of traps, one in either type of forest, were spaced 90 m apart; the primary forest set of traps and the secondary forest set of traps had a distance of 25 m and 17 m, respectively, from the border separating the two biomes. Each set consisted of six traps, arranged in two parallel lines of three each, that were separated by 10 m; within a line, traps came in 1 m intervals. Alongside each 3 trap-line and immediately adjacent to it, a blue polyethylene sheet of 25 cm height was erected as a 'guiding fence' to maximize capture success. The traps were made from 1.5 l water bottles owned by the 'Hidden Spring' company and formed by cutting off the neck of the bottle and then smoothly reinserting this part into the body in an inverted position to form a funnel of 9 cm length and a lower aperture of 4.5 cm (Fig. 1).

The funnel ensured that animals falling into the trap were retained. Escape by flight was negligible as it was never observed during observation stints (see below). The opening of the trap had a diameter of 9 cm and had a height of 20 cm above the bottom that was fitted with drainage holes to prevent

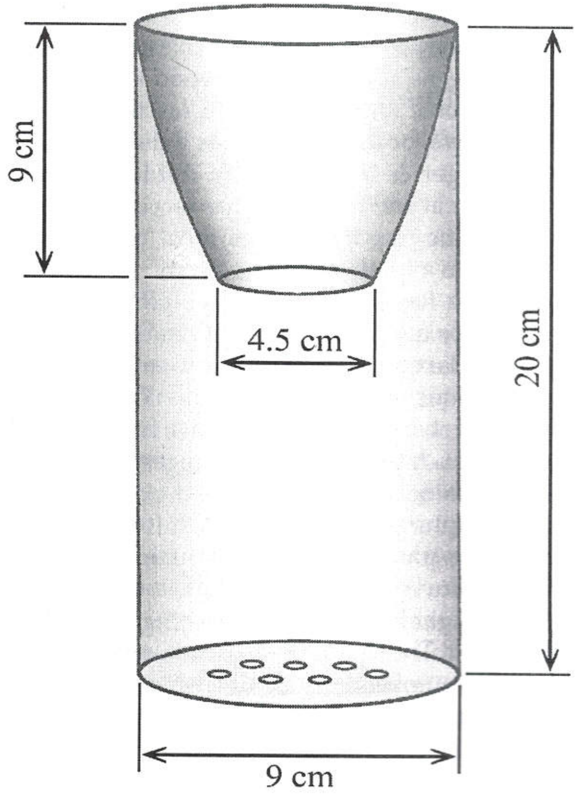

Figure 1. Pitfall trap made from plastic bottle. Drainage holes not drawn to scale.

the animals from drowning and the eventual evaporation of odorous rain water; the holes were sufficiently small as to retain even small invertebrates. In addition small stones placed on the bottom also forestalled the drowning of terricolines. (The restrictive collecting permit of the DENR prohibits indiscriminate killing/ collecting of any animal. Besides this would have run against the authors' ethics standard). Draining of water was further facilitated by digging the hole accommodating the trap deeper than dictated by the height of the bottle. Traps were sunk into the ground so that their lip came to lie level with the ground. When emptying a trap, it is taken up, its funnel removed, the catch counted and identified, and later released alive. Before repositioning a trap, the funnel is snugly attached in place again, and the soil adjacent to the lip carefully flattened as before. While thus shuttling the traps hence and forth, the observer wore latex gloves to prevent contaminating them and the surrounding soil with undesired odors. Furthermore, no insect-repellents were ever used before, during, or after field work, i. e. collecting and observation sessions.

The animals caught were screened twice a day, photographed where applicable, and scattered on the ground 5 meters away from the trap lines. Sometimes dead ants were found, likely the victims of others that had been trapped alongside (for an alternative explanation see Discussion). Terricolines were identified, at best, down to subfamily level because of the restrictions imposed on collecting (see above). Accordingly, only an epigaeic talitrid amphipod (Crustacea) species was collected for later identification.

Starting 18 March the traps were directly observed from a vantage point (hammock, plastic chair, standing still) while the observer, always the same person, minimized movement, vocalizing, and shading. From this vantage point, a 3 trap-line was monitored in front of the 'guiding fence' from a distance of ca. 1.5 m from the nearest trap. Observation stints in one forest lasted from 8.00 to 9.00 a.m. and from 16.00 to 17.00 p.m. and in the other from 9.05 to 10.05 a.m. and from 17.05 to 18.05 p.m. respectively. The sequence of observations in both habitats was randomized by flipping a coin before each 2 hr stint. During observations, every animal which happened to contact a trap's lip, enter and/ or exit a trap, or turn away from it upon sensing the 'cliff', was given a score; those exiting did so after a few seconds of walking around on the funnel wall facing upward. Animals exiting from the funnel and those turning away were scored 'avoiders', the captured ones 'captives'. With avoidance events of from 0 to 3 per hr observation, and even less captures, the observer never overtaxed in recording events completely, yet the surrounding litter may have led to some avoiders being overlooked by chance.

RESULTS

Captures comprised of Oligochaeta, Crustacea (1 talitrid amphipod species), Araneae, Myriapoda, Insecta and their larvae, including eight ant species [Formicinae]. The total number of captures was broken down into trap 'avoiders' and 'captives', as directly observed from seclusion, and the total numbers of captives, including those observed in the actual act of capture as retrieved from the traps (Table 1).

During direct observations there have been totals of 13 and 9 'avoiders' in primary and secondary forest, respectively (Table 1, B and C). Since the difference is not statistically significant (2-tailed binomial test, $p = 0.524$), samples were pooled. This total of 22 'avoiders' compares to totals of 1 and 5 observed actual 'captives' in both habitats during the same observation periods (Table 1, D and E). Since this habitat difference is likewise insignificant (2-tailed binomial test, $p = 0.218$), numbers from both habitats were pooled, thus yielding a total loss rate across all observation days of 78.6% (22 of 28 individuals). This indicates that the total number of 255 captives as retrieved from the 12 traps (Table 1, F) is possibly only a small fraction of the true number of potential captures. However, this total of all captures needs to be qualified.

First, since traps were left in place, a potential decrease in number of captives may have come about by some 'digging-in effect' because of faunal

Table 1. Daily numbers of individuals of terricoline invertebrates captured ('captives') with or repelled ('avoiders') by pitfall traps near Station Sibaliw, 2005. The effects of primary vs. secondary forest and day vs. night time.

	MARCH														APRIL		
A	18	19	20	21	22	23	24	25	26	27	28	29	30	31	01	02	?
B	3	1	1	0	1	1	1	0	1	1	0	0	0	2	0	1	13
C	1	2	0	1	1	2	0	0	0	0	0	0	2	0	0	0	9
D	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
E	0	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	5
F	19	24	15	20	25	11	16	12	15	21	11	21	13	13	19	--	255
G	0	0	0	0.5	1	0	0	0.5	0	0	0.5	0	0	0.5	0	--	3
H	0.25	0.3	0.35	-0.05	-0.7	0.35	0.35	-0.3	0.3	0.55	-0.05	0.45	0.25	-0.25	0.35	--	2.2
I	0.5	0.65	0.29	0.39	0.68	0.14	0.32	0.29	0.32	0.36	0.07	0.43	0.29	0.29	0.43	--	5.5

A: Dates of trap operation
B and C: Observed avoiders in primary and secondary forest, respectively; observations from two 1 hr stints/ day at 3 traps in each habitat pooled
D and E: Observed captives in two 1 hr stints / day with 3 traps in each habitat as in B and C
F: Total captives as retrieved from traps in both habitats during 24 hrs and 12 traps combined
G. Observed captives/ hr and 6 traps, with 3 in each habitat
H: Total captives / hr during daytime with 8 hrs observer-free operation of 6 traps, computed from the total obtained with all 12 traps in both habitats
I: Total captives/ hr during night time with 14 hrs observer-free operation of 6 traps in both habitats

depletion. Since captives were freed alive from their confinement twice a day and mortality in the traps was minute, any 'digging-in effect' must be spurious. Furthermore, a close inspection of numbers in the course of the whole observation period of 16 days (F) shows that numbers do not appear to decline.

Second, direct observations of the traps were confined to 10 hours of daytime so that it could be argued that in the night, i.e. in the remaining 14 hr, there may have been no avoiders, and consequently the tremendous loss rate reported above might have been mitigated. To test this possibility, day and night captures were compared. To make the most of the shorter sampling time period of 10 hr during daytime, the observer tried to determine whether 2 hr sampling in the presence of the observer (Table 1, G) may be combined with the 8 hr in the absence of the observer. To this end the number of all captives/hr recorded by the observer (G = 3) was compared to the total of observer-free captures/hr in the day (H = 2.2); negative values were derived by deducting the observed captives from the total number of captives. The difference between these two series of daily sample data is non-significant (2-tailed Mann-Whitney U test, n1, n 2 = 15, $p >> 0.05$). Therefore the data from both series were pooled to yield a summed up value of 5.2 captives/hr (G + H). Then the combined daytime captures/hr (G + H) were compared with the series of night time captures/hr (I = 5.5); the time period of 14 hr designated 'night time' also unavoidably included about 2 daytime, i.e. morning hours (from dawn at around 6 a.m. to 8 a.m. when observations at the traps started). The slight difference between the two series (5.5 vs. 5.2) is non-significant (2-tailed Mann-Whitney U test, n1, n 2 = 15, $p >> 0.05$). From this, one can conclude that trap efficiency does not differ across the light-dark cycle. At the same time, the lack of a difference between observer-free and observer-associated capture data (G vs. H) dispels the idea of a negative influence of the observer's presence on capture efficiency.

Aside from revealing the tremendous loss rate due to trap avoidance reported above, the data have a qualitative dimension as well. Had it not been for an observer at select times, certain taxa would have escaped our attention entirely. Thus a giant black formicine ant avoided the trap 4 times in primary forest (100% loss rate) and fell into the trap in half of 4 cases in secondary forest. Still more elusive was the behavior of a small black formicine ant and of a small spider that were seen to avoid a trap once in primary forest and secondary forest each, respectively. The latter two species had never been among the genuine captures. Potentially overlooking whole taxa would have been almost predicted from an overall loss rate of nearly 79% as inferred above from trap avoidance. Conversely, the talitrid amphipod collected would have been overlooked without trapping.

Finally, the capture data permit one to assess the habitat difference in what could be termed overall 'faunal abundance'. When data from pilot observations from 14 to 17 March and observed avoiders from 14 March to 02 April are added, and when from the respective observation periods 'captive' numbers (category F in Table 1) are extrapolated to 24 hr per work day, then there are collectively 371 captives in primary forest vs. merely 280 ones in secondary forest. Not surprisingly, there are significantly more individuals in primary than in secondary forest (2-tailed binomial test, $p = 0.0003$).

DISCUSSION

The major thrust of our findings is the low efficiency of Barber pitfall traps both in terms of species composition and overall capture rate. Though based on a limited study period of 16 days and a moderate number of 12 traps, the study stands out from previous work validating pitfall efficiency (Luff 1975, refs. in Southwood 1975, Seifert 1990, Laeger & Schultz 2005) by its naturalness: it combined dry pitfall trapping (see also Weeks et al. 1997) with direct observation from seclusion of events at the traps and maximized retaining efficiency by virtue of a funnel obstructing escape. Monitoring the behavior (turning away or entering the funnel with subsequent exiting vs. falling into the trap) replaces the inference based on distributional pattern from capture pattern with one based on *actual processes* in addition to capture pattern. This collective bonus revealed a tremendous overall loss rate of 79% of all terricolines that approached and eventually made contact with a trap. This figure is still conservative since a few potential 'avoiders' may have gone unnoticed in the surrounding litter.

In pioneer studies, both Seifert (1990) and Laeger & Schultz (2005) had carefully monitored the behavior of many ant species at pitfall traps independently from us, though they had used a preservative which confounds capture efficiency (Weeks et al. 1997). These ant studies came up with a remarkable number of confounding factors such as the 'self-rescue' and 'allo-rescue' of ants that have fallen into the preservative, ants using the traps as dumping site for dead conspecifics, the proximity of ant nests, to mention only a few. Incidentally, disposing of the dead may explain a sizeable (yet unrecorded) number of dead ants in our traps, which, if true, would tend to still further down-size our capture rate. Working with carabid beetles, and partly by direct observation in the lab, Luff (1975) revealed still other confounding factors such as an interaction of captive size and trap diameter.

Avoidance of and escape from traps apparently differs markedly among taxa. Seifert (1990) found capture rates for five ant species varying from 0.4% to 29.4% (median 4.3%) that translate into loss rates even bigger than the one found in the present study (see also Laeger & Schultz 2005). However, these studies and ours, the first critical pitfall assessment in a tropical setting, feature the same order of magnitude of trap inefficiency. For these reasons, pitfall trapping must be deemed inadequate when the research is aiming at assessing true species abundances. However, it is useful for obtaining a picture of the species composition of a terricoline community though even here a caveat is in place. While we would not have become aware of the terrestrial amphipod mentioned, we would have totally missed other taxa (see Results). Similarly, Weeks et al. (1997) collected 41 species only from kill traps, 12 were collected only from live traps and 32 were collected from both types of traps. Hence, even for the more qualitative portrayal of a coenosis, pitfall trapping needs to be applied very judiciously.

Our results have also shown that the primary forest terricoline coenosis is vastly richer in 'faunal abundance' (= number of captures) than that in the secondary forest, though the two collecting sites lay only 90 m apart. There was no major difference in taxonomic composition (not shown here) though one should recall that our identification scheme was usually not able to resolve differences below the level of the order. Yet even at this gross level of taxonomic resolution, the difference among the two forest biomes adds to the growing literature attesting greater biodiversity in primary forest as compared to any stage of succession of regrowth (Terborgh 1992, Phillips et al. 1994).

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