Pitfall trap efficiency: do trap size, collecting fluid and vegetation structure matter?

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Apart from experimental design, the selection of pitfall trap size, collecting fluid and habitat type sampled may also influence the capture efficiency of the method. We combined three field studies from two very different geographic areas, in which the efficiency of pitfall traps, using carabid beetles (Coleoptera: Carabidae), is evaluated. First, we showed that ethylene-glycol is a more efficient collecting fluid compared to commercial anti-freeze, paraffin and salt water in collecting beetles in a forest patch in South Africa. Second, we showed that larger traps (90 mm mouth diameter) are more efficient in collecting carabids than small traps (65 mm) in a meadow in Finland. We also showed that for these large traps, commercial vinegar was a better collecting fluid than propylene-glycol, but that for small traps, propylene-glycol was superior to vinegar in collecting carabids. Finally, we showed that the trappability of *Pterostichus oblongopunctatus* and *Carabus hortensis* differed in enclosures placed into two different habitat types (a forest and a clear-cut in Finland), while trappability did not differ significantly for two other species (*Calathus micropterus* and *Pterostichus niger*) in these habitat types. However, for the two *Pterostichus* species studied, the catches in traps placed in the centre of the enclosures were slightly higher in the clear-cut, compared to the forest, and catches were higher in enclosures with rich field-layer vegetation, compared to enclosures with poor vegetation. The three studies re-emphasise the uncertainties of using pitfall traps in ecological studies. However, with careful planning and standardisation to help avoid erroneous interpretations, pitfall trapping is an invaluable method for the field ecologist.

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1. Introduction

The use of pitfall traps for monitoring the number and activity of surface dwelling invertebrates is well known (Greenslade 1964, Luff 1975, Baars 1979, Halsall & Wratten 1988, Spence & Niemelä 1994, Ward *et al.* 2001), and the method has contributed substantially to our understanding of the pattern and comparative dynamics of epigaeic invertebrate assemblages. Pitfall traps are simple to use, inexpensive, provide a large return for time and money committed, and collect specimens continuously, including night foragers, so overcoming interspecific differences in circadian activity rhythms (Southwood 1978, Törmälä 1982, Samways 1983, Marsh 1984, Donnelly & Giliomee 1985, Huusela-Veistola 1996, Ward *et al.* 2001).

The application of the method has, however, not been without controversy (see Den Boer 1986). Criticisms of the method usually focus on its limited value in the direct estimation of population levels, or in comparing populations or assemblages (Southwood 1978, Den Boer 1986). Furthermore, species-specific behaviour in terms of movement activity periods and trappability (Greenslade 1964, Luff 1996) can bias results, even between species of the same genus (Mommertz *et al.* 1996). Pitfall trap catches are also influenced by climate, habitat structure, food availability, seasonally changing behaviour (which may differ between the sexes of a species), and even by the hunger level of the animal (Wallin & Ekbom 1994, Purvis & Fadl 1996).

The main factors that affect pitfall catches can be divided into three: trapping technique, structure of the habitat(s) to be sampled, and specific characteristics of the animals to be caught (Mommertz *et al.* 1996). Investigators have no control over the second and third factors, but do control trapping technique. Although there is no universally accepted placement and design of traps (Van den Berghe 1992), optimising these can improve efficiency. This was shown by Spence & Niemelä (1994) who compared capture efficiencies of different traps, and by Ward *et al.* (2001) who studied the effects of inter-trap distances on surface arthropod catches. Apart from placement and design, collecting fluid used can also strongly influence catches (Luff 1975, Holopainen 1992, Lövei & Sunderland 1996).

Using ground beetles (Coleoptera: Carabidae), a group commonly collected in pitfall traps, we investigated three questions, two of which involve pitfall trap design, and one habitat structure. First, we tested the relative efficiency of four pitfall-trap collecting fluids used commonly in the sampling of epigaeic invertebrates. These include an ethylene glycol:water (3:1) mixture, commercial anti-freeze, commercial paraffin, and salt water. Second, in a two-way design we tested the effects of pitfall trap size (65 vs. 90 mm mouth diameter) and collecting fluid (a propylene-glycol:water (1:1) mixture vs. commercial vinegar) on carabid beetle catches, both in terms of number of individuals and species collected, and in terms of species-specific trap efficiency. We expect the following from these two studies; (a) to collect more beetles in traps filled with ethylene or propylene glycol compared to traps filled with salt water (see Holopainen 1992 and references therein), commercial anti-freeze, paraffin or vinegar (probably because of the strong smells of these chemicals), and (b) to collect more individuals and species in the larger traps (because of the larger collecting area of these traps, see Brennan *et al.* 1999). Additionally, we quantify the ratio of male to female *Pterostichus niger* Schaller and *P. melanarius* Illiger individuals collected in the pitfall traps. These species were chosen because they are usually abundantly collected, and distinguishing sex is straightforward (see Lindroth 1985, 1986). True sex ratios are difficult to obtain from the literature, and the reported ones are based on pitfall catches. For example, Holopainen (1992) showed that in most carabid species collected by him, significantly more females were collected using ethylene glycol pitfall traps, while significantly more males were collected in some species where water-filled pitfall traps were used.

Third, we tested the efficiency of pitfall traps in different habitat types by comparing the number of released individuals of four carabid species (*Calathus micropterus* [Duftschmid], *Carabus hortensis* L., *Pterostichus oblongopunctatus* [F.] and *Pterostichus niger*) collected in enclosures placed in a forest patch and in a clear-cut. In unfenced habitat we expect to collect the first three forest dwelling species (Lindroth 1985, 1986) more frequently in forest habitat, and *P. niger* a forest/open-habitat generalist (Kinnunen 1999) in equal

numbers in forests and clear-cuts. This is because carabid beetles usually display random walking behaviour in favoured habitat, compared to directed movement behaviour in unfavourable habitat (Wallin & Ekbom 1988, Charrier *et al.* 1997). However, in the enclosures we anticipate the catches to be higher in the unfavourable habitat, because the enclosure walls may guide the beetles displaying directed movement behaviour into the pitfall traps placed at the enclosure corners, more so than for beetles which move randomly. This expectation is, however, conditioned on the assumption that overall beetle activity is unchanged from favoured to unfavourable habitat. If not, we anticipate a difference in carabid catch in the traps in the centre of the enclosures (i.e. traps not influenced by the enclosure walls) in the different habitat types.

2. Material and Methods

2.1. Collecting fluid study

This part of the study was performed in the Karkloof forest-block (29°19´S 30°16´E), KwaZulu-Natal, South Africa. This forest-block forms part of the greater mistbelt-forest complex, which is situated on the southeastern slopes of the Drakensberg mountain range. The study site was dominated by the following tree species: Cape plane (*Ochna arborea*), Outeniqua yellowwood (*Podocarpus falcatus*), Henkel's yellowwood (*P. henkelii*), White violet-bush (*Rinorea angustifolia*), Sneezewood (*Ptaeroxylon obliquum*), Common spike-thorn (*Gymnosporia buxifolia*), Common turkey-berry (*Canthium inerme*) and Lemon wood (*Xymalos monospora*). Traps were visited four times, twice a month, between the beginning of October and the end of November 1997, the South African spring season.

Plastic pitfall traps used had a mouth diameter of 75 mm and a depth of 85 mm. A gridsect trap layout was used to collect the ground beetles. Sixteen grids were placed along a line transect within a Karkloof forest patch. Each grid consisted of 16 traps, arranged in four sets of four (Fig. 1a). Four commonly used collecting fluids were used here: an ethylene glycol:water (3:1 ratio) mixture, commercial antifreeze (with ethylene glycol as a major component), commercial paraffin, and salt water. Distances between traps, sets and grids are shown in Fig. 1a. Unfortunately the four traps per set, i.e. the collecting fluids, were not placed randomly, and the traps were placed rather close to one another so that the collecting fluids used may influence the catch in adjacent traps. We discuss these problems later.

A one-way ANOVA was used to test the null hypothesis of no difference in carabid abundance and species richness between the four collecting fluids used.

2.2. Trap size and collecting fluid study

In 1999 we placed 40 pitfall traps in a meadow (homogeneous to the human eye) near Nuuksio National Park (60°16´N 24°40´E), southern Finland. The study site was a moist meadow with scattered willows (*Salix* spp.), where the main plant genera were *Agrostis*, *Alopecurus*, *Calamagrostis*, *Hierochloe* and *Phleum* grasses. *Filipendula*, *Hypericum*, *Vicia* and *Trifolium* species were also abundant. *Brachytecium* mosses were abundant in dry areas where the grasses did not cover the whole bottom layer. Trapping started on 7 June 1999 with traps visited twice (7 July, 10 August 1999), the Finnish summer season.

Pitfall traps were placed in five line transects (10 m apart), each line containing eight traps (8 m apart). Twenty traps were large (90 mm mouth diameter), and 20 were small (65 mm mouth diameter). In 20 traps we placed commercial vinegar as collecting fluid, and in 20 a propylene-glycol:water (1:1) mixture. This resulted in 10 large traps with a propylene glycol:water mixture, 10 large traps with vinegar, 10 small traps with a propylene-glycol:water mixture and 10 small traps with vinegar. A systematic design (Fig. 1b) was employed to avoid inadequate interspersion of traps, a problem sometimes associated with randomisation designs in small experiments (Hurlbert 1984).

Data were analysed using a Model I two-factor ANOVA, with trap size and collecting fluid as factors. *Pterostichus melanarius* and *P. niger* sex ratios were calculated on the mean numbers of individuals collected from the 20 small traps (propylene-glycol and vinegar fluids pooled), and from the 20 large traps (propylene-glycol and vinegar traps pooled) separately. Sex ratios from small and large traps were calculated separately because trap size had a significant effect on catch, while collecting fluid appeared not to influence catch (see Results section and Table 2b).

2.3. Habitat type study

This part of the study was done in Lammi (61°04´N 24°54´E), southern Finland, during the summer of 2001. We selected a recently clear-cut stand (approximately 2–3 hectares; logged 1.5 years before the experiment) with an adjacent mature forest stand. Both stands represented a *Myrtillus*-type (Cajander 1949) forest, where Norway spruce (*Picea abies* [L.] Karst.) is the dominant tree species in the mature phase. The field layer was mainly dominated by *Calamagrostis* and *Deschampsia* grasses in the clear-cut, and *Vaccinium myrtillus* and *V. vitis-idaea* dwarf shrubs in the forest stand.

We placed eight 2 × 2 m enclosures (styrene panels, 30 cm high, no roof cover, partly dug into the ground layer) in the clear-cut and eight in the forest stand (Fig. 1c). The enclosure material was hard and smooth and thus probably prevented the beetles from escaping from the enclosures. Four enclosures in each habitat type were in sites where the field-layer vegetation was well developed (percentage cover between 50% and 100%), and four were in sites which only

a - 1997

Grid 16

Grid 3

Grid 2

10 m

10 m

A B   A B
● ●   ● ●
C D   C D   2 m
● ●   ● ●

Grid 1   5 m

A B   A B
● ●   ● ●
C D   C D   2 m
● ●   ● ●

2 m   5 m   2 m

A = Ethylene-glycerol
B = Anti-freeze
C = Paraffin
D = Saltwater

b - 1999

40 m

LV1	SV1	LG1	SG1	LV2
LG3	SG2	LV3	SV2	LG2
SV3	LV4	SG3	LG4	SV4
SG5	LG5	SV5	LV5	SG4
LV6	SV6	LG6	SG6	LV7
LG8	SG7	LV8	SV7	LG7
SV8	LV9	SV9	LG9	SV10
SG10	LG10	SG9	LV10	SG8

56 m

L – Large traps (90 mm mouth diameter)
S – Small traps (65 mm mouth diameter)
V – Vinegar
G – Propylene-glycol:water

c - 2001

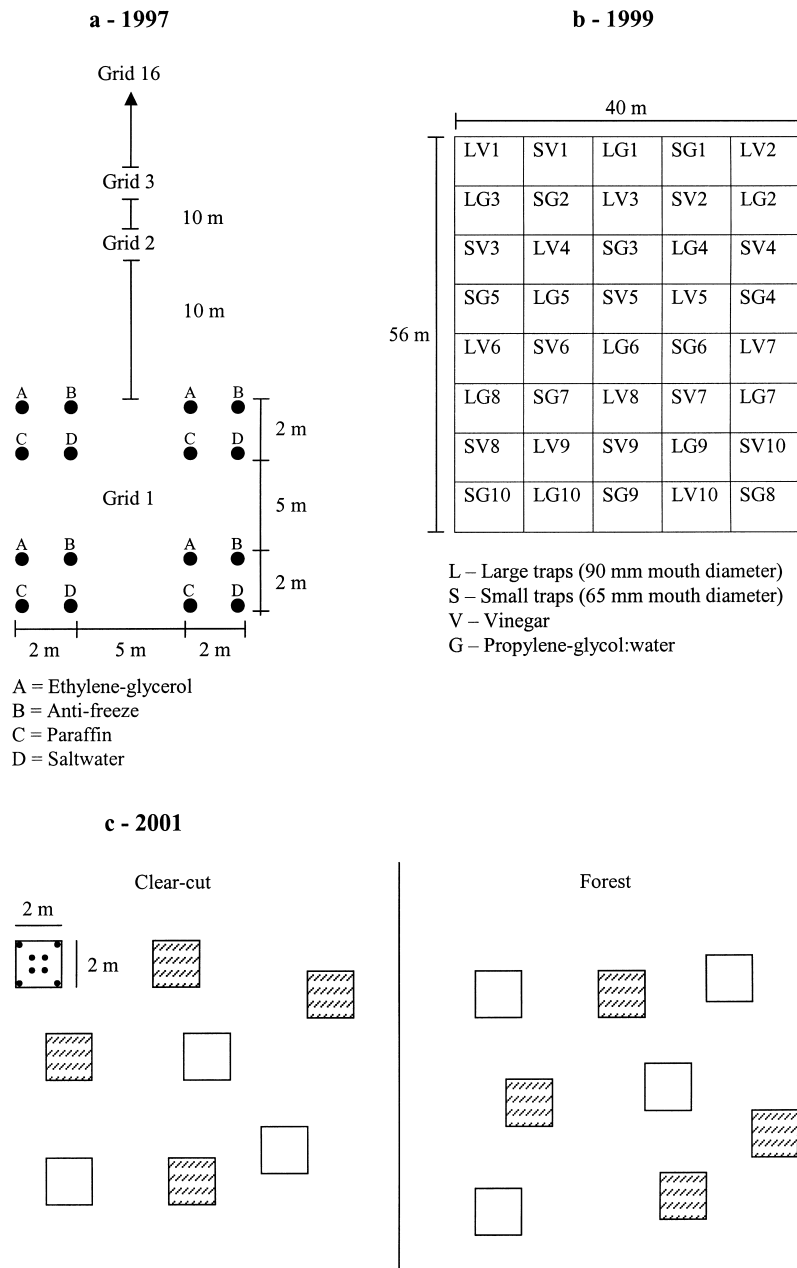Clear-cut   Forest

2 m

2 m

Fig. 1. The three study designs. — a. Gridsect sampling design in a homogeneous forest patch in Karkloof forest, South Africa, 1997. Each grid consisted of 16 traps arranged in four sets of four with the four collecting fluids placed within each set. — b. Sampling design in a field near Nuuksio National Park, Finland, 1999, testing the effects of collecting fluid and trap size on carabid catch. — c. Sampling design in Lammi, Finland, 2001, using 2×2 m enclosures (with eight traps per enclosure) to test trappability in poorly (open squares) and well-developed (shaded squares) field layers in clear-cut and forest.

had mosses and litter on the soil surface but no or little field-layer vegetation (percentage cover less than 10%). Thus, we had four enclosures representing sites with no forest cover and scarce field-layer vegetation, four with no forest cover but where the field-layer vegetation was well developed, four with forest cover but scarce field-layer

vegetation, and four with forest cover and abundant dwarf shrubs. We placed eight dry pitfall traps (mouth diameter 80 mm, depth 105 mm) into each enclosure: one in each corner, and four traps (1×1 m square) in the centre of the enclosure. The traps were covered with styrene roofs (10×10 cm) in order to protect them from litter and rain. The immediate surroundings (5–10 cm) around each trap were cleared from field-layer vegetation.

Since the enclosures had no roofs, we focused the study on flightless carabid species. We collected individuals from sites next to the enclosures, and randomised them before releasing; for example, an individual caught from the clear-cut was not necessarily released there. Each individual was marked by using model paint and nail varnish, before release into an enclosure. We released a total of 234 individuals of *Calathus micropterus*, 64 individuals of *Pterostichus oblongopunctatus*, 48 individuals of *P. niger* and 32 individuals of *Carabus hortensis* into the enclosures (Table 1). We released beetles in equal amounts into each enclosure in three release periods.

The release periods were separated by 'kill' pitfall trapping (salt water; between the periods), and we trapped out before the release experiment. We, therefore, assume that the density of individuals was not too high within the enclosures. In the 'kill' trapping before the experiment, for example, we caught from some enclosures as many as 12–14 individuals of *P. oblongopunctatus*. This leads to a minimum 'natural' density estimate of over 3 individuals/m², which is approximately the same or even higher than that in the experiment.

Because of several zero catches during the catch periods, we pooled the dataset (recapture events per enclosure) but kept the species separate. The data were analysed using a Model I two-factor ANOVA, with field-layer vegetation (rich or poor) and habitat type (clear-cut or forest) as factors.

3. Results

3.1. Collecting fluid study

Carabid beetles are, taxonomically and ecologically, poorly known in South Africa, with the last major revision of the whole group more than a century ago (Péringuey 1896). Subsequently, we grouped the carabids collected here into 16 morphospecies (see Oliver & Beattie 1993, 1996), with a collective abundance of 197 individuals.

Significantly more carabid individuals and species were collected from traps filled with the ethylene-glycol:water mixture than those with any other collecting fluid (Table 2a, Fig. 2). Traps filled with paraffin collected the lowest mean number of individuals and species. These results should be considered with caution because of an error in the experimental layout, i.e. even as great care was taken into placing the traps in homogenous forest habitat, a pre-existing field gradient might have obscured these results (Hurlbert 1984). The 'left-hand side' of the experimental layout only had traps filled with ethylene-glycol and paraffin, while the 'right-hand side' of the layout only had traps filled with anti-freeze and salt water (see Fig. 1a). To correct for this mistake we should have randomised each set of four pitfall traps. Nevertheless, we did not observe obvious environmental gradients in the study area and are quite confident in the results presented here.

In absolute numbers, traps filled with ethylene-glycol:water trapped 101 (50% of total catch) individuals and 11 (69%) species, with commercial anti-freeze 46 (23%) individuals and 7 (44%) species, with commercial paraffin 10 (5%) individuals and 6 (38%) species, and with salt water 40 (20%) individuals and 8 (50%) species.

3.2. Trap size and collecting fluid study

A total of 43 carabid species and 1417 individuals were collected here (Appendix). *Pterostichus*

Table 1. Carabid individuals released into the experiment enclosures during the trapping periods in 2001. Release = total number of individuals released, Capture = total number of recapture events during the period. Captured beetles were re-released into the enclosures (and the same individual may thus have been caught more than once), which explains the sometimes higher number in Capture than in Release columns.

Species	4–15 June		15–24 July		16–23 August	
	Release	Capture	Release	Capture	Release	Capture
Calathus micropterus	96	12	192	31	48	7
Carabus hortensis	–	–	–	–	32	119
Pterostichus niger	–	–	48	96	16	39
P. oblongopunctatus	64	47	–	–	–	–

Table 2. Analysis of variance results. — a. One-way ANOVA testing for differences in carabid beetle catch in four different collecting fluids. — b. Model I two-factor ANOVA testing for differences in catch using two different collecting fluids and two different trap sizes. F = females, M = males. — c. Model I two-factor ANOVA testing for differences in catch of four carabid species in poorly and well-developed field layers (Field layer) in a clear-cut and forest patch (C_F).

Source of Variation	df	MS	F	p
a. Collecting fluid study (KwaZulu Natal, South Africa)				
Carabid abundance				
Collecting fluid	3	1.109	15.831	< 0.001
Error	60	0.070		
Carabid species richness				
Collecting fluid	3	16.224	12.064	< 0.001
Error	60	1.345		
b. Trap size and collecting fluid study (Espoo, Nuuksio, Finland)				
Carabid abundance				
Collecting fluid	1	0.090	0.207	0.652
Trap size	1	5.326	12.203	0.001
Collecting fluid × Trap size	1	2.297	5.263	0.028
Error	36	0.436		
Carabid species richness				
Collecting fluid	1	0.591	0.100	0.754
Trap size	1	101.602	17.146	< 0.001
Collecting fluid × Trap size	1	12.812	2.162	0.150
Error	36	5.926		
Pterostichus melanarius (F)				
Collecting fluid	1	0.206	0.116	0.736
Trap size	1	6.525	3.663	0.064
Collecting fluid × Trap size	1	5.075	2.849	0.100
Error	36	1.781		
Pterostichus melanarius (M)				
Collecting fluid	1	0.139	0.097	0.757
Trap size	1	12.344	8.592	0.006
Collecting fluid × Trap size	1	4.749	3.306	0.077
Error	36	1.437		
P. niger (F)				
Collecting fluid	1	0.004	0.007	0.935
Trap size	1	5.471	9.337	0.004
Collecting fluid × Trap size	1	0.276	0.471	0.497
Error	36	0.586		
P. niger (M)				
Collecting fluid	1	0.005	0.013	0.911
Trap size	1	3.514	8.363	0.006
Collecting fluid × Trap size	1	1.174	2.795	0.103
Error	36	0.420		
Carabus nemoralis				
Collecting fluid	1	0.709	1.091	0.303
Trap size	1	0.017	0.026	0.873
Collecting fluid × Trap size	1	0.134	0.206	0.653
Error	36	0.650		

Table 2. Continued.

Source of Variation	df	MS	F	p
Trechus secalis				
Collecting fluid	1	1.202	0.918	0.344
Trap size	1	0.029	0.022	0.883
Collecting fluid × Trap size	1	2.237	1.709	0.199
Error	36	1.309		
c. Habitat type study (Lammi, Finland)				
Calathus micropterus				
C_F	1	0.046	0.533	0.480
Field layer	1	0.001	0.017	0.899
C_F × Field layer	1	0.004	0.047	0.832
Error	12	0.086		
Carabus hortensis				
C_F	1	0.127	4.444	0.057
Field layer	1	0.003	0.103	0.754
C_F × Field layer	1	~ 0	0.007	0.933
Error	12	0.028		
Pterostichus niger				
C_F	1	0.012	0.645	0.437
Field layer	1	0.001	0.058	0.814
C_F × Field layer	1	0.045	2.384	0.149
Error	12	0.028		
P. oblongopunctatus				
C_F	1	0.826	10.446	0.007
Field layer	1	0.103	1.302	0.276
C_F × Field layer	1	~ 0	~ 0	0.984
Error	12	0.079		

a — abundance data log-transformed; species richness data not transformed.
b — abundance data log-transformed; species richness data not transformed, *Pterostichus melanarius* (F), *P. melanarius* (M), *P. niger* (F), *P niger* (M) and *Carabus nemoralis* — square-root transformed; *Trechus secalis* — Ln-transformed.
c — data log-transformed.

melanarius was the most abundantly collected species with a total number of 712 (50% of total catch) individuals. *Trechus secalis* (289 individuals, 20%), *P. niger* (112 individuals, 8%) and *Carabus nemoralis* (38 individuals, 3%) were also collected in sufficient numbers to test for differences in trappability.

There was a statistically significant effect of trap size on the catch in most cases, while in most analyses performed we did not detect an effect of collecting fluid on the catch (Table 2b). Overall, large traps collected significantly more individuals (Fig. 3a) and species (Fig. 3b) than small traps. For large traps, however, the vinegar collecting fluid appeared to be more efficient than the pro-pylene-glycol mixture, while for small traps propylene-glycol was more efficient.

Large traps collected more male and female individuals of *P. melanarius* and *P. niger* (Fig. 3c–f) compared to small traps, although the difference was not statistically significant at the 5% risk level for *P. melanarius* females. We did not find a significant effect of either trap size or collecting fluid on the numbers of *C. nemoralis* (Fig. 3g) and *T. secalis* (Fig. 3h) collected. Although mostly statistically non-significant, there was a tendency in all analyses performed for a higher catch in large traps filled with vinegar (compared to large traps filled with propylene-glycol), and a higher catch in small traps filled with pro-
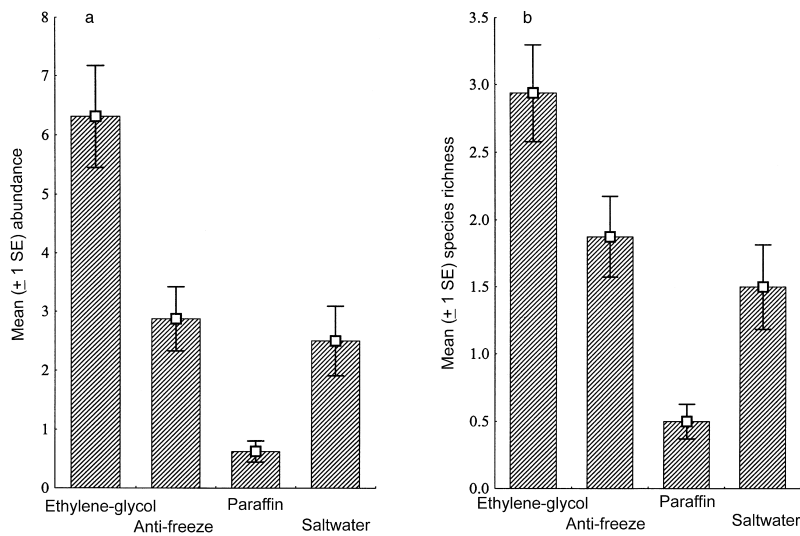
Fig. 2. — a. Mean number (±1 SE) of carabid individuals collected by using four collecting fluids (ethylene-glycol:water mixture, commercial anti-freeze, commercial paraffin and salt water). — b. Mean number of species (±1 SE) of the same study.

pylene-glycol (compared to small traps filled with vinegar) (Fig. 3).

Sex ratios of *P. melanarius* were close to parity, but for *P. niger* more females than males were collected in both small and large traps. In the small traps, we collected a mean of 7.54 ± 1.46 SE *P. melanarius* females, and 6.26 ± 1.17 SE males (1.2:1 female:male sex ratio), while in the large traps we collected a mean of 11.42 ± 1.75 SE females, and 12.80 ± 1.72 SE males (0.89:1 sex ratio). For *P. niger*, we collected a mean of 0.78 ± 0.12 SE females and 0.57 ± 0.13 SE males (1.37:1 sex ratio) in the small traps, and 2.54 ± 0.56 SE females and 1.92 ± 0.39 SE males (1.32:1 sex ratio) in the large traps.

3.3. Habitat type study

The ANOVA results indicate that trappability was not significantly different among the treatments for three of the four species studied, and that the field-layer vegetation had no detectable effect for all four species studied (Table 2c, Fig. 4). However, for *P. oblongopunctatus* the catches were significantly higher in the clear-cut than in the forest. The catches of *C. hortensis* were slightly, albeit statistically non-significant at the 5% risk level, higher in the forest than in the clear-cut enclosures.

These results may indicate differences in movement behaviour in the forest and clear-cut, because directed movements may potentially lead to higher catchability than random walk in traps that have guiding walls. By looking at the mean values of the centre traps (i.e. excluding the traps at the enclosure walls) for the two *Pterostichus* species, we indicate that the above results may also be explained by factors other than simply directed or random movement — in general, the centre-trap catches were lower in shady habitats. In the forest-clear-cut comparisons, the catches of these species were higher in the clear-cut — for *P. oblongopunctatus*, the mean catch was 1.25 ± 0.65 SE in the clear-cut and 0.38 ± 0.18 SE in the forest enclosures ($n = 13$), and for *P. niger* the respective catches were 2.50 ± 0.60 SE and 1.38 ± 0.46 SE ($n = 31$). Moreover, when comparing sites with scarce field-layer vegetation to sites with well-developed field-layer vegetation, for *P. oblongopunctatus* the mean catch was 0.50 ± 0.19 SE in the former and 1.13 ± 0.67 SE in the latter, and for *P. niger* the respective catches were 1.75 ± 0.49 SE and 2.13 ± 0.64 SE.

4. Discussion

Pitfall trapping is the most popular, and most frequently used field method for studying carabid beetles (Lövei & Sunderland 1996). Consequently, it is important to realise the shortcomings of the method and, where possible, to improve it. Our aim was to highlight some of these
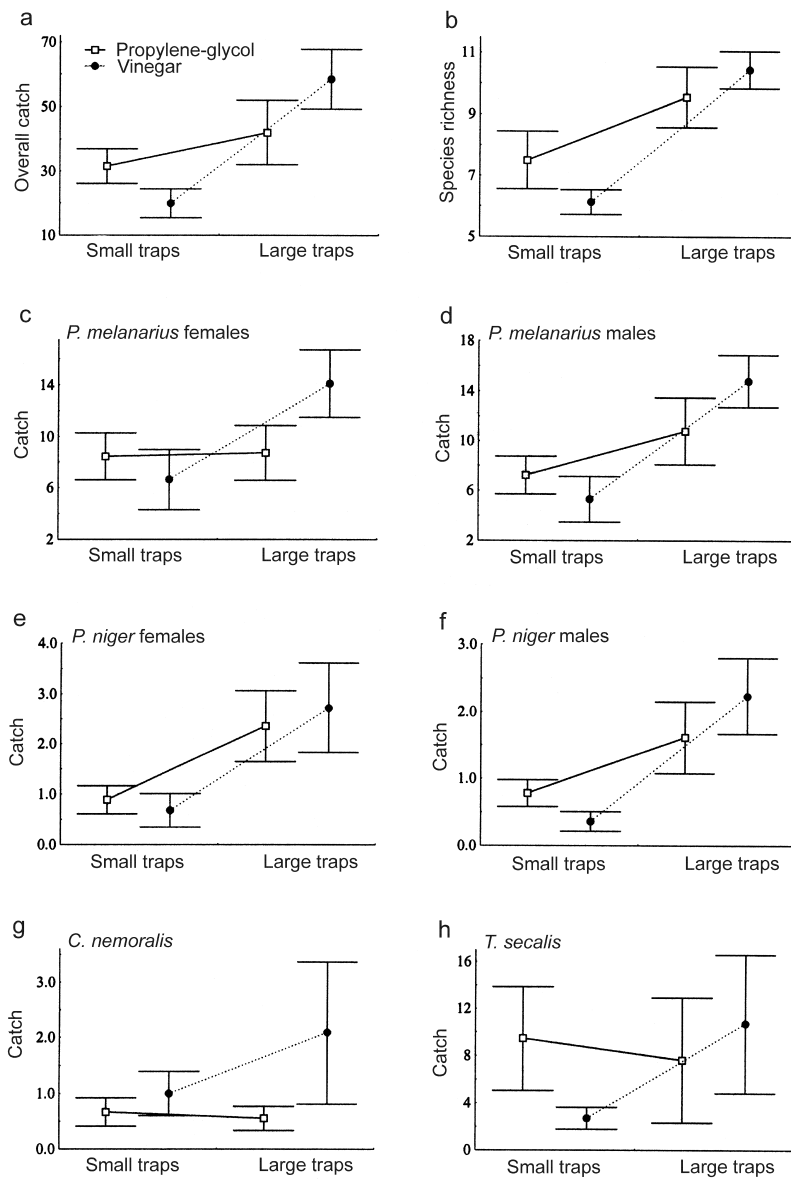
Fig. 3. Mean catches (±1 SE) in small vs. large traps and in traps with propylene-glycol vs. vinegar as collecting fluid. — a. Overall catch. — b. Species richness. — c. *Pterostichus melanarius* females. — d. *P. melanarius* males. — e. *P. niger* females. — f. *P. niger* males. — g. *Carabus nemoralis.* — h. *Trechus secalis.*

issues, with the following results; (1) collecting fluid used and the size of the trap played important roles in determining carabid catches of pitfall traps, (2) we found no significant difference in the number of male and female individuals of *Pterostichus melanarius* or *P. niger* collected in pitfall traps, and (3) the trappability of pitfall traps in different habitat types (here a forest and clearcut) in enclosures depended on the species trapped. For example, *P. oblongopunctatus* and to a lesser degree *C. hortensis* showed differences in catchability between habitat types, while *Calathus micropterus* and *P. niger* showed little differences between the habitat types sampled. Field-layer vegetation had no detectable effect on the catches.

4.1. Towards an optimal trap use: the importance of collecting fluid and trap size

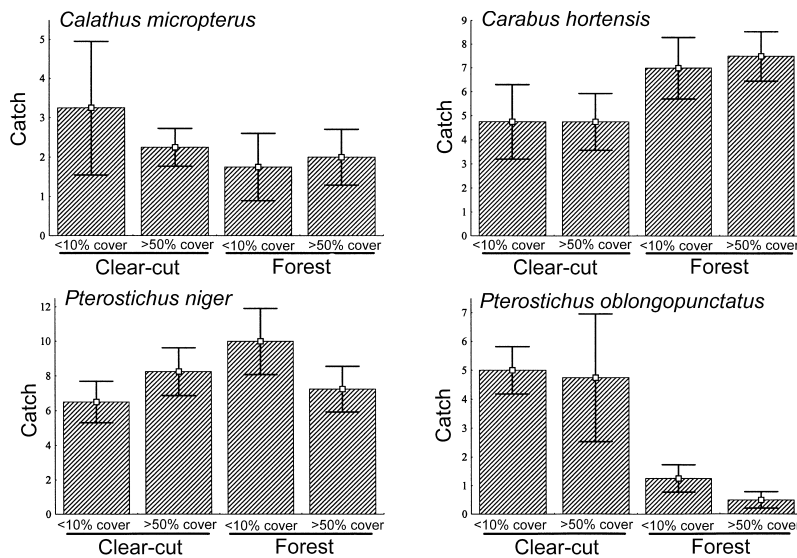Our results indicate that water-diluted glycol appears to be the best alternative when using pitfall

Fig. 4. Mean catches (±1 SE) of *Calathus micropterus*, *Carabus hortensis*, *Pterostichus niger* and *P. oblongopunctatus* in poorly (< 10% cover) and well-developed (> 50% cover) field layers in a clear-cut and a forest patch.

traps. Glycol was also more efficient in collecting carabid beetles than was salt water, a result also found by Holopainen (1992) in a forest nursery at Suonenjoki, central Finland. In general, the result may indicate that strong smelling liquids are avoided by carabids, but to our knowledge no information is available on the repelling or attractive effects of collecting fluids. Collecting efficiency also seems to vary depending on trap size.

As expected, large traps were more effective in catching carabids than smaller ones. Large traps were also shown to be optimal in collecting spiders in a Western Australian Jarrah forest (Brennan *et al.* 1999). There are, however, three not mutually exclusive reasons for not using very large pitfall traps. First, many small mammals (mice, shrews and voles) were found in large pitfall traps, but almost none in the smaller ones. Brennan *et al.* (1999) also found this and suggested that smaller traps might be more appropriate, as long as these traps are sufficiently large to collect the largest species of the target taxon. Moreover, trapping animal groups other than the target taxa may have ethical implications. Second, traps filled with decaying small mammals might influence catches by attracting e.g. carrion beetles (Silphidae) and flies (Diptera: Calliphoridae and Muscidae), and even carabid beetles. Therefore, we recommend researchers to use traps with mouth diameter 60–70 mm rather than larger traps,

to keep the trap size constant in a given study, and perhaps to use mesh wire around the trap edges. Third, if smaller traps are more efficient in collecting small beetles, compared to large traps (see Luff 1975), it is advisable to use these small traps, as most carabid species are small. For example, of the 402 carabid species occurring in Fennoscandia, 311 (77%) are smaller than 10 mm in size. In our second study (carried out near Nuuksio National Park), the percentages were 64 and 36, respectively (for beetle sizes see Lindroth 1985, 1986). The danger here, of course, is that the use of small traps may exclude the capture of larger carabid species. However, in the Nuuksio study the catches of small and large traps were not statistically different for the large *C. nemoralis* and the very small *T. secalis*. Perhaps the best strategy is to establish the body-size range of the local species pool *a priori*, and then to perform a pilot study to establish the 'optimal' trap size, i.e. a trap that will collect small and large species efficiently.

One aspect not considered in this study is that of trap depth. Deep traps may catch more small mammals than shallow traps, as escaping from the deep ones may be more difficult. Brennan *et al.* (1999) suggested that larger beetles can escape from small traps, not because of their small trap mouth diameter, but because small traps are also shallower and when occasional leafs fall into these small traps, it is easier for larger beetles to

escape. A way to try to separate these two effects would be to design an experiment using traps with the same mouth diameter but different trap depths.

4.2. The unbearable complexity of comparing pitfall catches of different habitats

Several examples exist of studies where pitfall catches of two (or more) rather different habitats were compared without taking into account potential differences in beetle catchability between these habitat types. For example, Honek (1988) showed that the pitfall catches were higher in sparse than in dense field-layer vegetation, and Siemann *et al.* (1988) showed that the vegetational richness correlated positively with the richness of invertebrate catches. Moreover, Lenski (1982) and Niemelä *et al.* (1993) compared pitfall catches of carabids in mature and clear-cut stands. Results like these should be treated cautiously, as they might only reflect differences in the moving behaviour of beetles in different habitat types (Wallin & Ekbom 1988, Charrier *et al.* 1997), rather than real differences in numbers between habitats. Surprisingly, in the enclosures it appeared that the structure of the field-layer vegetation had no detectable effect on the total number of recapture events, but the presence of a tree canopy did influence trappability. Although only suggestive, this indicates that the moving behaviour of carabid beetles changes when they encounter unsuitable habitat, more so than when they encounter architectural differences in vegetation structure within a habitat type.

Our results at first hand perhaps mostly indicate whether a given species used random or directed movements in the clear-cut, the latter movement behaviour resulting in a higher catch because of increased probability in hitting the enclosure walls and, further, to be guided into the traps that were placed in the corners next to the walls. This may imply that, when using guiding walls around the traps, the comparability of catches of different habitat types is low — probably lower than using traps without the walls.

With the present experimental design we cannot exclude the possibility that the catchability of traps in forests and clear-cuts (or in sites with well and poorly developed field-layer vegetation) are different: in traps *not* placed next to the enclosure walls, the catches of two *Pterostichus* species were higher in the clear-cut than in the forest enclosures, and higher in enclosures with rich than poorly-developed field-layer vegetation. Moreover, Charrier *et al.* (1997) showed that radio-tracked individuals of the forest carabid *Abax parallelepipedus* were inactive for shorter periods and moved longer distances in the favoured forest habitat, compared to other habitats. Therefore, a crucial question concerning the effect of habitat on catches is whether the 'direction' of the effect can be predicted. At first this seems to demand only knowledge on the habitat specificity of a given species, and on the microclimatic conditions of the studied habitat types. For example, light, moisture and wind conditions may vary considerably between mature forest and clear-cut stands (Matlack 1993). As was shown for two *Pterostichus* species (Baars 1979) and for the chrysomelid beetle *Trirhabda borealis* (Goodwin & Fahrig 2002), beetles may be more active and use directed movements in unfavourable conditions (lack of food, poor habitat, etc.), increasing the likelihood of capturing individuals in the enclosures placed in these unfavourable habitats. However, it is also known that carabid beetles move randomly in favoured habitat (Wallin & Ekbom 1988, Charrier *et al.* 1997), thereby increasing the likelihood of being captured.

This dilemma in predicting the effect of habitat on carabid activity is a serious one. Most obviously is the fact that we may not be able to reliably predict the activity or density of a particular species in a particular habitat type, using pitfall traps. This is because local activity and density are likely to be influenced by temperature, how starved the beetle is, whether there is shelter around, and a myriad of other obvious and not so obvious factors. Alternatively, beetle habitat associations recorded in the literature could be incorrect (being often based on biased pitfall-trapping comparisons), and once accurate information on a carabid beetle's 'preferred' habitat is available, better predictions may be possible. Radio-tracking or mark-recapture techniques might be reliable solutions for comparing different types of habitat and to shed more light on species habitat associations.

4.3. Ecological findings and conclusions

In our habitat study, there were also important ecological findings. We showed that *P. niger* and *C. micropterus* were quite evenly captured from different types of forest habitats. This supports Kinnunen (1999) and Heliölä *et al.* (2001), who showed that *P. niger* is a habitat generalist (with respect to canopy closure) and the same probably holds true for *C. micropterus* in the clear-cuts (logged 1–2 years earlier) and mature, closed stands. Furthermore, the primary literature classifies *P. oblongopunctatus* as a forest species (Lindroth 1986), even though Koivula (2002) caught it almost equally abundantly in mature-forest and in clear-cut stands (with the same forest type as in our study). Concerning the centre traps, we collected this species more frequently from the clear-cut than from the forest, and more often from enclosures with rich than from those with poor field-layer vegetation. These discrepancies in catch frequency may make conclusions regarding the differences in the carabid faunas of different habitats difficult and unreliable. Finally, although more *C. hortensis* individuals were captured from forest enclosures, supporting results from Niemelä *et al.* (1993) and Koivula (2002), this species may also tolerate logging and survive in the clear-cuts, at least in the short term.

Although this paper deals with pitfall trapping, the same problems (of liquid used, trap size and habitat) probably affect other passive trapping methods. The results of *P. oblongopunctatus* and *C. hortensis* indicate that there are problems in comparing within-species catches (let alone between two or more different species) from different environmental types. This point is accentuated in a study by Desender & Maelfait (1986) who showed that carabid beetle captures in pitfall traps in enclosures were much better correlated to catches in soil samples — thought of as a reliable density estimate — than to catches in open pitfall traps. There are, however, no straightforward solutions for this (except for testing the effect of the studied habitats for every species), since for large-effort studies there are no realistic (cheap and easy) alternatives to pitfall trapping.

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Appendix. Carabid beetles collected near Nuuksio National park, Finland. Prop-glyc = propylene-glycol.

Species	Size (mm)	Small traps		Large traps	
		Prop-glyc	Vinegar	Prop-glyc	Vinegar
Agonum fuliginosum (Panzer)	6–8	4	1	8	3
Agonum obscurum (Herbst)	5–7	–	–	1	–
Amara aenea (Degeer)	6–9	5	2	1	2
Amara communis (Panzer)	6–7	3	–	19	14
Amara curta Dejean	6–7	–	–	–	1
Amara eurynota (Panzer)	10–13	–	–	1	2
Amara famelica Zimmermann	7–9	1	–	–	–
Amara lunicollis Schiødte	7–9	1	–	10	11
Amara montivaga Sturm	8–9	–	–	1	–
Amara nitida Sturm	7–9	–	–	–	1
Amara quenseli (Schönherr)	6–9	–	–	1	2
Amara tibialis (Paykull)	4–6	–	–	1	–
Anisodactylus binotatus (F.)	10–13	–	–	–	1
Bembidion guttula (F.)	3–4	6	6	8	2
Bembidion lampros (Herbst)	3–4	1	1	–	5
Bembidion minimum (F.)	2–3	1	–	2	–
Bembidion properans (Stephens)	3–4	–	–	1	–
Bembidion quadrimaculatum (L.)	3–4	–	–	2	–
Bradycellus caucasicus (Chaudoir)	3–4	–	–	–	1
Carabus granulatus L.	16–23	–	–	–	1
Carabus hortensis L.	22–28	–	1	3	2
Carabus nemoralis Müller	22–26	6	8	5	19
Clivina fossor (L.)	6–7	–	1	2	2
Dromius sigma (Rossi)	3–4	–	–	–	3
Harpalus latus (L.)	8–11	–	–	3	–
Harpalus rufipes (Degeer)	10–17	–	–	2	2
Harpalus tardus (Panzer)	8–11	–	–	2	–
Lebia chlorocephala (Hoffmann)	6–8	–	–	1	1
Leistus terminatus (Hellwig *in* Panzer)	6–8	1	–	–	1
Loricera pilicornis (F.)	6–9	1	3	1	3
Patrobus assimilis Chaudoir	8–9	–	1	2	–
Patrobus atrorufus (Ström)	7–10	1	–	3	2
Pterostichus cupreus (L.)	11–13	2	1	5	6
Pterostichus diligens (Sturm)	5–7	1	2	–	1
Pterostichus melanarius (f) (Illiger)	12–18	76	59	84	136
Pterostichus melanarius (m) (Illiger)	12–18	65	46	104	142
Pterostichus niger (f) (Schaller)	15–20	8	6	23	27
Pterostichus niger (m) (Schaller)	15–20	7	3	16	22
Pterostichus nigrita (Paykull)	9–13	–	1	3	–
Pterostichus oblongopunctatus (F.)	10–12	–	1	–	2
Pterostichus strenuus (Panzer)	6–7	5	3	6	4
Pterostichus versicolor (Sturm)	9–12	3	2	4	33
Trechus micros (Herbst)	4–5	1	–	–	–
Trechus secalis (Paykull)	4	85	23	75	106
Trichocellus placidus (Gyllenhal)	4–6	–	–	2	–