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Litter disturbance and trap spatial positioning affects the number of captured individuals and genera of crickets (Orthoptera: Grylloidea)

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Abstract

There are several factors that may affect sampling with pitfall traps. Here we test the hypothesis that the mere walking of the researcher proximate to the traps could cause an increment in the capture of crickets. This would occur if the walking provoked vibration in the litter, to which crickets showed a jumping response, thus falling into the pitfall traps. We mounted 126 traps in 14 groups of nine. The traps within a group were positioned in three parallel rows of three traps each, one meter apart from each other. Each group of nine traps was separated from the other groups by at least 5 m. Each group of nine traps was submitted to one of seven levels of disturbance frequency. Exposure time was 7 d for all traps. Treatments (disturbance frequencies) were allocated randomly among trap groups. For the data analyses we adjusted mixed-effects polynomial models. We captured 723 cricket individuals, distributed in 10 genera, most in the nymphal stage. As expected, the number of captured individuals, as well as the number of genera, increased with disturbance frequency. However this response was not linear: at higher disturbance frequencies there was a decrease in captures. There was also an effect of trap positioning within each group: central traps were more affected by disturbance than peripheral ones, while peripheral traps captured more individuals and genera in the absence of disturbance. Therefore we recommend areas near pitfall traps not be visited during the trapping period. Alternatively, to enhance sampling efficiency, the researcher may do programmed visiting to the trapping area, but this must be rigorously designed to provoke exactly the same disturbance for all traps. Enhancing the distance among traps will augment efficiency in capturing individuals and capture larger cricket diversity. Further studies of the interaction between methodology and cricket behavior will refine our ability to design and interpret pitfall studies.

Key words

litter disturbance, pitfall trap, spatial positioning, crickets, jumping response, substrate vibration

Introduction

Pitfall traps have been used extensively to sample ground-dwelling arthropods (Southwood 1978). Pitfalls have been more commonly used for carabid beetles (Briggs 1960; Luff 1968, 1975; Digweed *et al.* 1995) and ants (Sackmann & Farj-Brener 2006; Borgelt & New 2006; Ribas *et al.* 2005; Schoereder *et al.* 2004a, b), but also for mole crickets (Tsurikov 2006, Barbara & Buss 2006, Adjei *et al.* 2003), and true crickets (Carmona *et al.* 1999, Simpson *et al.* 1992, Ribas *et al.* 2005, Velez & Brockmann 2006). Crickets have sometimes been used to test ecological hypotheses (Ribas *et al.* 2005, Mendes & Sperber 2003), insofar as they are the most common Orthoptera in tropical forest litter (Desutter-Grandcolas 1995).

Though pitfall trapping remains the most widely used and

practical method available for sampling epigaeic arthropods, it incorporates many possible biases (Adis 1979, Digweed *et al.* 1995). It is known that pitfall catches can be affected by trap size and shape (Luff 1975, Adis 1979, Spence & Niemelä 1994), type of preservative (Luff 1968, Sperber *et al.* 2003), physical structure of the environment (Greenslade 1964, Durkis & Reeves 1982), and time of trap disposition (Niemelä *et al.* 1990).

Catches are often highest soon after pitfall traps are inserted into the soil, which has been termed a “digging-in effect” (Greenslade 1973). In a previous work, Mendes and Sperber (2003, pers. obs.) observed that pitfall traps collected twice within a disposition period of five days, captured more crickets than traps collected only once during the same period. This led to the hypothesis that crickets could be responding to the vibration of the litter substrate, provoked by researchers walking to the traps. Traps collected twice would receive a greater frequency of substrate vibration than traps collected once, (the latter visited only on trap insertion into the soil and on final trap collection). In response to substrate vibration the crickets would jump, falling into the nearby pitfall traps. The same process could be generating a “digging-in” effect on these organisms. The work reported here aimed to test the prediction that cricket captures in pitfall traps, provoked by walking among the traps, would increase with the disturbance frequency.

Methods

Study area and experimental design.—The study took place in an Atlantic forest remnant (secondary submontaneous semideciduous forest), called Mata da Biologia (Jardim Botânico da UFV) in Viçosa, Minas Gerais State, Brazil (long 20°45'S, lat 42°50'W) in April 2006. We mounted 126 pitfall traps: translucent plastic vials, of 10-cm diameter and 10-cm depth. The traps were positioned in groups of nine (Fig. 1), in a total of 14 groups. Each group was placed in the middle of a 7 × 7-m quadrat, subjected to a particular experimental disturbance frequency (treatment), with two replicates per disturbance level (number of days with disturbance). The allocation of treatment levels to the quadrats was done randomly. Traps remained mounted in the field for seven days. There was a total of 882 trap-days sampling effort.

The experimental disturbance consisted of a daily walking by the researcher (LGSS), following always the same route, as depicted in Fig. 1. Each group was disturbed one to seven times during the sampling period: all groups were disturbed on the first sampling day, all but the groups assigned disturbance level “1 day with distur-

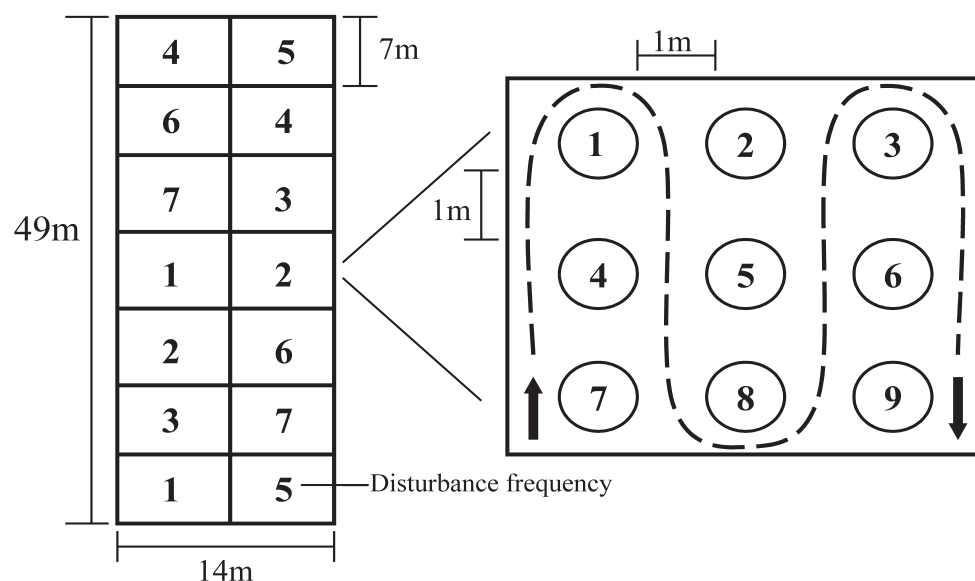


Fig. 1. Diagram of disturbance treatments' layout in the field. On the left the disposition of the 14 trap groups (replicates), with treatment levels (numbers within each square represent disturbance frequencies) assigned at random. On the right the disposition of pitfall traps within each group, traps numbered from one to nine, and the walking route used to make the disturbance (dashed line, arrows indicate walking direction).

Table 1. Analysis of variance of maximal models, to explain cricket (Orthoptera, Grylloidea) abundance or diversity per pitfall trap. Adjusted models: mixed effects, polynomial ANCOVA. Significance assessed by Restricted Maximum Likelihood Estimation (REML). Response variables: Abundance = \log ('number of individuals per trap'+1); Diversity = \log ('number of genera' + 1); Disturbance = number of days with disturbance; Trap position = central or peripheral; Disturbance quadratic term = squared disturbance; df=degrees of freedom. Maximal models: $Y \sim \text{Intercept} + \text{Disturbance} + \text{Trap position} + \text{D2} + \text{Interaction of Disturbance with Trap position}$.

Response variables	Source	Numerator df	Denominator df	F	p
Abundance	Intercept	1	109	755.18	<.0001
	Disturbance	1	11	2.22	0.16
	Trap position	1	109	1.42	0.24
	Disturbance quadratic term (D2)	1	11	11.49	0.006
	Disturbance: position	1	109	6.19	0.01
	D2: position	1	109	0.72	0.40
Diversity	Intercept	1	109	1307.18	< 0.0001
	Disturbance	1	11	0.14	0.72
	Trap position	1	109	9.73	0.002
	Disturbance quadratic term (D2)	1	11	6.75	0.02
	Disturbance: Position	1	109	9.93	0.002
	D2: Position	1	109	0.33	0.57

Table 2. Analysis of variance of minimal adequate models to explain cricket (Orthoptera, Grylloidea) abundance or diversity per pitfall trap. Adjusted models: mixed effects, polynomial ANCOVA. Significance assessed by Restricted Maximum Likelihood Estimation (REML). Response variables: Abundance = \log ('number of individuals per trap'+1); Diversity = \log ('number of genera' + 1); Disturbance = number of days with disturbance; Trap position = central or peripheral; Disturbance quadratic term = squared disturbance; d.f.=degrees of freedom; * explanatory term maintained in the minimum model because it was present in the significant interaction. Minimal adequate models: $Y \sim \text{Intercept} + \text{Disturbance} + \text{Trap position} + \text{D2} + \text{Interaction of Disturbance with Trap position}$.

Response variables	Source	Numerator df	Denominator df	F	p
Abundance	Intercept	1	110	755.18	<.0001
	Disturbance	1	11	2.22	0.16 *
	Trap position	1	110	1.42	0.24 *
	Disturbance quadratic term (D2)	1	11	11.49	0.006
	Disturbance: position	1	110	6.21	0.01
Diversity	Intercept	1	110	1307.18	<.0001
	Disturbance	1	11	0.14	0.72 *
	Trap position	1	110	9.79	0.002
	Disturbance quadratic term (D2)	1	11	6.75	0.02
	Disturbance: position	1	110	9.99	0.002

bance" were disturbed on the second day; all but disturbance level "2" were disturbed on the third day and so forth, up to disturbing only the two groups with disturbance level "7" on the last day, just before collecting traps. Therefore disturbance level "1" corresponds to those two groups disturbed only on the first day; disturbance level "7" corresponds to those two groups disturbed once every seven sampling days. To estimate diversity, the crickets were identified to genus level. Separation to the lower taxonomic level of species depends on adult male genitalia analysis and this was not possible because most collected crickets were in the nymphal stage.

Data Analysis.—We used two response variables for cricket captures: number of captures of individuals per trap (abundance) and number of captured cricket genera per trap (diversity). Both response variables were transformed to $\log(x+1)$, because they are counts (Zar 1974), and analyzed in separate univariate models.

We adjusted polynomial linear mixed-effects models (LME procedure), analogous to an analysis of covariance (ANCOVA), using pitfall groups as random effects ($n=14$). The use of mixed-effects models permitted us to test the effects of trap spatial positioning, without incurring any pseudoreplication error (Crawley 2002). We considered as fixed effects the disturbance frequency (number of disturbance days), a quadratic term for disturbance (days squared), trap spatial positioning (categorical variable), and the interaction of the continuous with the categorical variables (see Table 1).

We added a quadratic term for disturbance because we expected a nonlinear response of crickets to disturbance frequency. At low disturbance levels, cricket abundance and diversity would increase linearly with disturbance; at higher disturbance levels we expected there would be a decrease in cricket response to disturbance.

Trap spatial positioning was evaluated in two alternative forms: we evaluated if there was an effect of positioning related to the walking route of the researcher, considering the traps placed in the intermediate line (traps number 2, 5, 8 in Fig. 1) *vs* those in the lateral lines (traps 1, 4, 7, 3, 6, 9 in Fig. 1). In a separate model, we evaluated if traps placed centrally (trap number 5 in Fig. 1) presented a different response than peripheral traps (trap numbers 1, 2, 3, 4, 6, 7, 8, 9 in Fig. 1). To choose between the two alternative trap positioning variables, we compared the Akaike Information Criterion (AIC, Crawley 2002) of the respective minimal adequate models. The Akaike Information Criterion, also called penalized log likelihood, is useful to compare alternative models because it explicitly penalizes any superfluous parameter in the model by adding $2p$ (p = number of parameters in the model). When comparing two models, the smaller the AIC, the better the fit (Crawley 2002).

Maximal models included all factors, interactions and covariates that might be of any interest (see Table 1). Maximal models were simplified by removing nonsignificant terms, so as to achieve minimal adequate models. Significance (5%) of term removal was evaluated using maximum likelihood (ML), as recommended to compare mixed-effects models with different fixed effects (Crawley 2002). Significance of the terms in the minimal adequate models was evaluated by analysis of variance tables, using Restricted Maximum Likelihood Estimation (REML) instead of maximum likelihood, because maximum likelihood underestimates the size of the variance components (Crawley 2002). All analyses were done using the statistical package R (R Development Core Team, 2005).

Results

We collected 723 individual crickets, almost all nymphs, distributed in 10 genera (number of individuals in parens): *Amanayara* de Mello & Jacomini (26), *Phoremia* Desutter-Grandcolas (459) and *Zucchiella* de Mello (44) (Nemobiinae: Trigonidiidae); *Ectecous* Saussure (180), *Laranda* Walker, F. (1), *Izecksohniella* de Mello (1), *Eidmanacris* Chopard (3) (Phalangopsidae); one genus of Mogoplistidae (7) and two genera of an unidentified Grylloidea family (2).

The minimal adequate models using trap line as categorical explanatory variable (intermediate *vs* lateral) presented larger AIC values (individuals: AIC = 206.67; genera: AIC = 73.13) than the models using spatial positioning (central *vs* peripheral) as categorical explanatory variable (individuals: AIC = 203.16; genera: AIC = 65.14). Therefore we opted for the models using spatial positioning (central *vs* peripheral) as most adequate to explain both the number of cricket individuals and genera.

In Table 1 we present the results of the analysis of variance of the maximal models for cricket abundance and diversity. The interaction of trap position with the quadratic term of disturbance was not significant for either cricket abundance or diversity (Table 1). For both abundance and diversity, the minimal adequate models (Table 2) included the disturbance frequency, the quadratic term for disturbance frequency, trap spatial positioning and the interaction of positioning with disturbance frequency. For cricket abundance, although the effect of disturbance was not significant alone, we maintained it in the minimal model because its interaction with positioning was significant. For cricket diversity, the minimal adequate model (Table 2) also included the disturbance frequency, a quadratic term for disturbance frequency, trap spatial positioning (central *vs* peripheral), and the interaction between trap positioning and disturbance. The effects of disturbance and trap positioning were maintained in the model because of the significant interaction term. The fitted parameter values of the minimal adequate models are presented within Fig. 2 (for abundance) and Fig. 3 (for diversity).

Cricket abundance increased with disturbance frequency, up to a maximum of five to six days of disturbance, diminishing in trap groups with higher disturbance frequencies (Fig. 2). Central traps were differently affected by disturbance than peripheral ones: up to a disturbance frequency of 3 d: peripheral traps captured more individuals than central ones, while with disturbance levels greater than 4 d, central traps captured more individuals (Fig. 2). Analyzing the fitted parameter values for the minimal model (equations in Fig. 2), we observed that (i) there is capture of crickets, even without disturbance (the estimated intercepts were larger than zero), (ii) peripheral traps captured more crickets than central traps when there was no disturbance (the intercept for peripheral traps was larger than that for central traps), (iii) disturbance led to an increase in the capture of crickets (the estimated parameter values for the effect of disturbance frequency were all positive), (iv) high frequencies of disturbance reduced the number of captured individuals (the parameter value for the quadratic term of disturbance was negative), and (v) the effect of disturbance upon capture was smaller on peripheral than central traps (the parameter value estimated for disturbance effect on peripheral traps was smaller than that for central traps).

The diversity of captured crickets increased with disturbance frequency (Fig. 3), however peripheral traps captured higher diversity than central traps at almost all disturbance frequencies. And there was a tendency for reduction in diversity, particularly in the

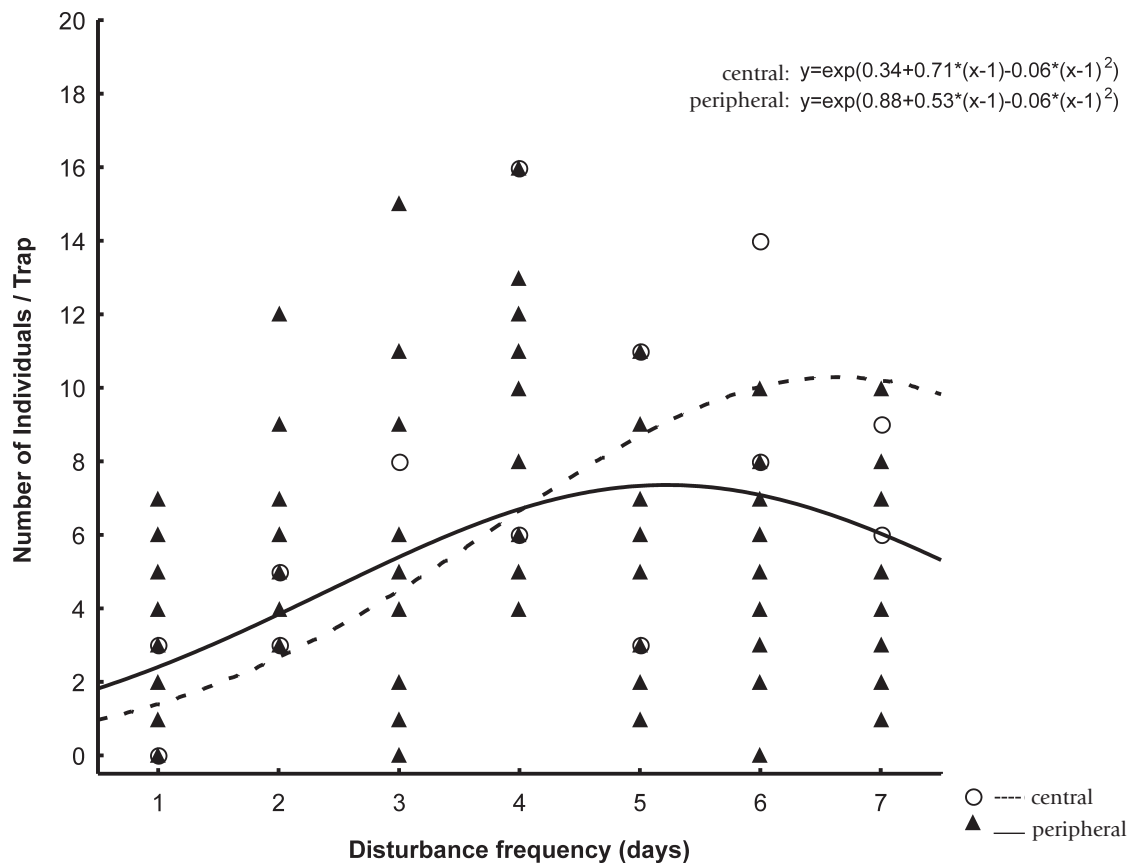


Fig. 2. Number of individual crickets captured per pitfall trap as a function of disturbance frequency (days). Open circles and dashed line represent central traps; triangles and solid line represent peripheral traps. Equations present the parameter values estimated for the minimal adequate statistical model.

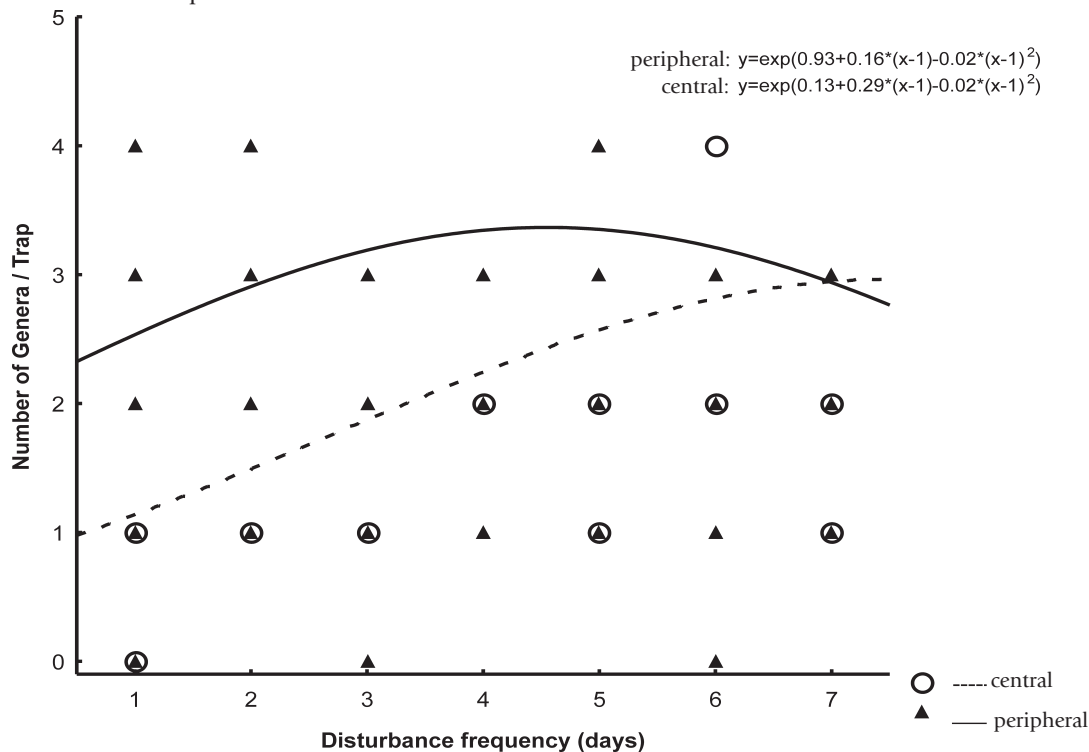


Fig. 3. Number of cricket genera captured per pitfall trap as a function of disturbance frequency (days). Open circles and dashed line represent central traps; triangles and solid line represent peripheral traps. Equations present the parameter values estimated for the minimal adequate statistical model.

peripheral traps, with high disturbance frequencies. The analysis of the estimated parameters of the minimal adequate model (equations in Fig. 3) showed the same qualitative results as for the number of captured individuals.

Discussion

Other authors have studied the effect of disturbance upon pitfall catches (Joosse & Kapteijn 1968, Digweed *et al.* 1995, Ribas *et al.* 2005), but the effects were either used as bioindicators of habitat disturbance (Topping & Lövei 1997, King *et al.* 1998, Ribera *et al.* 2001), or when experimentally manipulated, the disturbance was of a greater degree than that studied here (*eg.*, Digweed *et al.* (1995) moved the traps). Our results show that merely walking proximate to mounted pitfall traps is sufficient to increase the number of captured crickets, as well as their diversity. This result is already observed for Collembola (Joosse & Kapteijn 1968).

Our interpretation is that visitation provokes vibration of the litter, triggering a jumping response of crickets. Orthoptera present a startle response to vibration (Friedel 1999) which may have been selected for as an escape response to predators. For many arthropods, vibrations traveling through the substrate are important in the detection of predators and prey (Brownell 1977, Barth *et al.* 1988, Pfannenstiel *et al.* 1995, Meyhöfer *et al.* 1997, Coccoft *et al.* 2000).

A portion of the jumping crickets fall in the traps, contributing to the total number of captured individuals, as well as to the captured cricket diversity. This effect occurs probably to a decreasing extent in relation to disturbance frequency: the first disturbance would lead to the highest number of jumping crickets [analogous to the "digging-in" effect described for ants by Greenslade (1973)], while subsequent disturbances would lead to a decreasing number of jumping crickets because of a decrease in the number of available cricket individuals in the area proximate to each trap. This local decrease is a phenomenon analogous to the depletion (reduced catch) evaluated by Baker & Barmuta (2006) and Digweed *et al.* (1995) for litter beetles.

However this mechanism alone does not explain the quadratic response of cricket captures in relation to disturbance frequency. If this mechanism acted alone, we would expect the best-adjusted response of capture numbers to disturbance frequency would be an asymptotic one, with capture numbers stabilizing as exhaustion occurred in the availability of crickets in the area proximate to the traps.

Recall that the response variable — the number of captured individuals or genera — is accumulated capture across the whole experiment. Therefore those traps that were not visited in the last days had already accumulated the captures of the previous four to five days with disturbance, as similarly for the traps visited all seven days. These traps must have captured an additional number of individuals greater than that captured in the traps visited more frequently. Although the decrease in the adjusted curves (Figs 2, 3) could be interpreted as an artifact inherent to the use of the quadratic term in the adjusted model, we discard this hypothesis because there was an actual decrease in the number of captured individuals and genera in the traps visited most frequently, compared to those visited during four to five days (Figs 2, 3).

We interpret the decreasing effect of disturbance on capture numbers as resulting from a second biological process, independent of the jumping response of crickets. The jumping response alone leads to an increased capture with disturbance. We suggest that the

biological process that responded negatively to disturbance frequency was the recolonization of the area, occurring when there was no disturbance. This recolonization would be slower than the jumping response, contributing to a lower number of captured individuals per day, but surpassing the number of jumping crickets when disturbance frequency is higher than four days.

Colonization ability of the bushcricket *Metrioptera roeseli* (Orthoptera, Tettigoniidae) was studied in relation to propagule size (number of colonizing individuals) (Berggreen 2001) and landscape composition (Berggreen *et al.* 2001), introducing individuals experimentally into habitat islands previously uninhabited by the species. Natural colonization was recorded for *Dolichopoda* cave crickets (Orthoptera, Rhaphidophoridae) (Bernardini *et al.* 1997). In terrestrial ecosystems, recolonization has been studied after disturbance caused by clearcutting and fire (Clayton 2002), and by mining (Majer *et al.* 1984, Majer 1996, Sieg *et al.* 1987). Recolonization from neighboring areas, may be an adaptive strategy for survival of crickets in seasonally inundated tropical forests (Sperber & Adis 2007). To our knowledge however, there is no study on such a local and short-period response as that shown here. Saltatorial insect, such as crickets, may show a particularly quick recolonization after low-intensity disturbances because of their behavioral response.

Why were central traps differently affected by disturbance than peripheral ones? We suggest that these results arise partially from the walking route taken by the researcher, but we discard the statistical model that includes line positioning *per se* in place of the spatial positioning (central *vs* peripheral) of the trap. We suggest that the inadequacy of this model occurred because the intermediate line of traps included both the more disturbed traps due to the researcher's walking route, and also two peripheral traps. We suggest that the whole intermediate line of traps is more affected by disturbance, but this effect is counterbalanced in the two outer traps of the intermediate line because of their peripheral positioning.

The capture might therefore, be affected by two mechanisms. One mechanism is the jumping response of crickets to disturbance; the other is the greater capture of crickets in peripheral traps because of the effect of spatial positioning. Support for this interpretation is that simultaneously there was a steeper effect of disturbance on central traps, as shown by the larger estimated parameter values for disturbance effect on central *vs* peripheral traps, and allied with this a larger intercept estimated for peripheral than central traps (Figs 2, 3).

The larger capture from peripheral traps, in the absence of disturbance (estimated intercepts) is an edge effect resulting from their external spatial positioning: these peripheral traps should intercept more cricket jumps than central traps because they draw upon trap-free edges and therefore intercept cricket jumping from a larger surround than the central traps (each of which are surrounded by eight other traps). The peripheral traps capture crickets jumping both from inside the trapped area and from outside it.

The response of capture diversity with increasing disturbance frequency seems to follow a similar pattern to the number of individuals, but with a lag. The adjusted curves for diversity are similar to those for individuals, up to a disturbance frequency of 4 d. The adjusted parameter values for diversity indicate a decrease in captured diversity should occur for disturbance frequencies higher than 7 d, as did occur for disturbances higher than 4 d in the number of captured individuals. Therefore, both for the number of captured individuals as for the number of captured genera, there was a 'hump shaped' response curve, with a lag in the maximal response in the peripheral compared to the central traps. In peripheral traps we

found larger diversity, probably because the captured crickets came from a larger area in comparison to the central traps. Peripheral traps may capture crickets jumping from all the area surrounding the trap group, while central traps only capture crickets coming from a more limited area (as above). As well as for individuals, the reduction in captured diversity at higher disturbance frequencies is the same for central and peripheral traps. We credit this reduction to a reduced recolonization in the trap groups that were disturbed more frequently.

The retardation in the response of diversity, compared to the response of abundance, results probably from a sampling effect: there have to be lots of captured individuals to detect a change in diversity. This is an extension of the well-known species-area relationship, which shows that the estimated diversity increases with sampling effort (Connor & McCoy 1979, Krebs 1999, Lomolino 2000, Schoereder *et al.* 2004b).

We conclude that disturbance and trap spatial positioning affect the number of captured crickets, as well as their estimated diversity. We recommend that when using pitfall traps to sample crickets, the area near the traps should not be visited during the trapping period. Alternatively, to enhance sampling efficiency, the researcher may do programmed visiting to the trapping area, but this visitation must be rigorously designed, so that it provokes exactly the same disturbance for all traps. Traps positioned comprising a larger area will be more efficient in capturing individuals and will capture larger cricket diversity. Further studies of the interaction between pitfall methodology and cricket behavior will help to refine our ability to design and interpret pitfall studies with crickets.

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