

## CHAPTER 11

*THE DESIGN OF PROGRAMS TO MONITOR FOREST  
BIODIVERSITY: LESSONS FROM THE WOG WOG  
HABITAT FRAGMENTATION EXPERIMENT*

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**INTRODUCTION**

Measuring and monitoring forest biodiversity is an expensive activity requiring a commitment of funds and personnel over long periods of time. It is important, therefore, to make certain that the questions being asked can be answered. One of the keys to success is the design of the monitoring program.

A sound design should provide unequivocal answers. Alternative interpretations need to be rigorously excluded. Many monitoring activities involve some form of treatment; for example, logged *versus* unlogged forest or fragmented *versus* continuous forest. Most studies utilize existing treatments, so it can be difficult to determine whether differences recorded during monitoring are due to the treatment or to pre-existing differences in the untreated forest. To minimize such problems, the design phase of a monitoring program should include the following elements, demonstrated by Bormann and Likens (1979), Likens (1985), and others as necessary for monitoring programs:

- (1) controls in untreated forest;
- (2) treatment replicates to account for spatial heterogeneity and random variation and to provide error estimates;
- (3) pre-treatment monitoring to establish natural trends in the features being monitored and any pre-treatment differences between plots;
- (4) environmental stratification to detect any interactions among treatments and environmental variables;
- (5) a sufficient period of monitoring to establish treatment effects and distinguish them from climatic fluctuations or other episodic events; and
- (6) replication at more than one location to avoid location-specific phenomena.

Practical impediments will usually make it necessary to compromise. However, at the outset the question should always be asked: Do cost, or other practical constraints limit the design to such an extent that useful results are unlikely to

be forthcoming? If the answer is yes, then scarce research resources should probably be spent asking questions that have a better chance of being answered (Nicholls and Margules, 1991).

In this paper we demonstrate the relevance of design factors to forest biodiversity monitoring programs, using some results obtained from a field experiment on habitat fragmentation that has been underway for 10 years, along with the benefit of hindsight. The results themselves are not interpreted here. Rather, they are used to illustrate the importance of certain design principles. The design of monitoring programs should include, as a minimum, control and replication to improve the likelihood that the programs will deliver ecologically meaningful results with stated estimated levels of confidence. In this way, the cost-effectiveness of future monitoring programs might be improved.

### THE WOG WOG EXPERIMENT

The Wog Wog habitat fragmentation experiment commenced in the southern summer of 1984/1985. The experiment was established in response to the research agenda (Haila, 1986; Saunders *et al.*, 1991) set by the equilibrium theory of island biogeography (MacArthur and Wilson, 1967). Its objectives are twofold: to test the prediction that smaller habitat fragments retain fewer species than larger ones, holding distance to source populations approximately constant; and to identify which species are susceptible to habitat fragmentation and why.

A full description of the experiment and a rationale for the design are given in Margules (1992); for a summary see Margules *et al.* (1994). Figure 11.1 shows the location and the spatial arrangement of the experiment. There are 18 forest plots, representing three sizes – 0.25 ha, 0.875 ha, and 3.062 ha – replicated six times. Monitoring commenced in February 1985. The experimental treatment began in April 1987 and was completed in December 1987. The treatment involved clearing the forest surrounding replicates one to four and establishing a plantation of *Pinus radiata*. Replicates five and six remained as controls in the adjacent continuous forest (Figure 11.1).

There are eight monitoring sites in each of the 18 plots (for a total of 144 sites), in both the continuous forest controls and the fragments. The location of each monitoring site was determined by stratifying on the basis of slope or drainage line (local habitats) and center or edge of plot (called inner and outer zones). The monitoring sites are replicated at the lowest stratum. Thus, there are two inner drainage line sites and two outer drainage line sites, plus two inner slope sites and two outer slope sites. Following the fragmentation treatment, an additional 44 monitoring sites were established outside the forest fragments. At each monitoring site, a pair of pitfall traps is opened for seven days each season (four times each year). In this way, populations of ground-dwelling arthropods and small vertebrates are monitored.

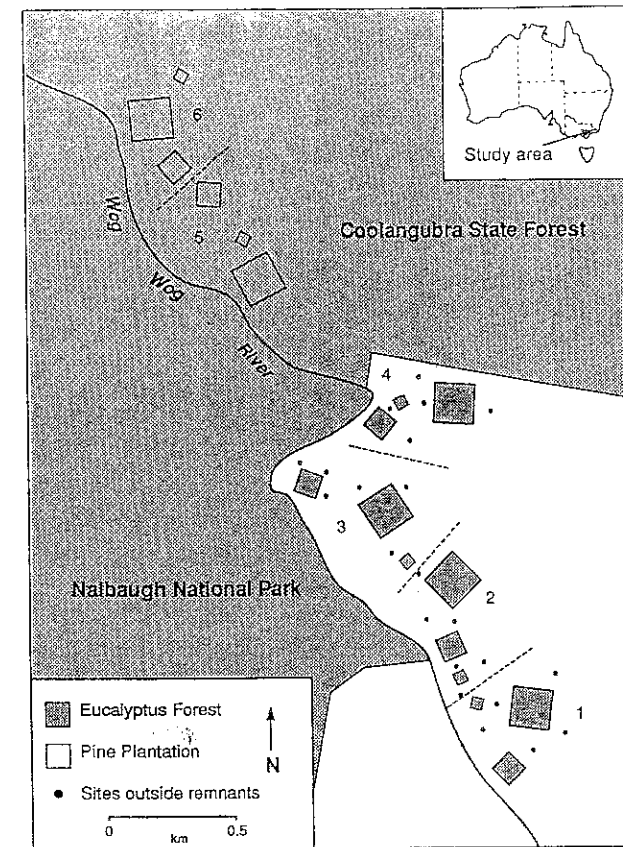


Figure 11.1 Location and layout of the Wog Wog habitat fragmentation experiment, showing the four replicate sets of forest remnants and the two replicate sets of controls in continuous forest. The dots represent the approximate locations of monitoring sites established between and around the forest remnants after the fragmentation treatment

### RESULTS TO DATE

To date, the effects of habitat fragmentation and fragment size have been tested on an amphipod (Family Tallitridae) and a scorpion (*Cercophonius squama*) (Margules *et al.*, 1994), eight beetles (Family Carabidae), the frog *Crinia signifera* (Margules *et al.*, 1995), and three millipedes (*Gephyrodesmus* sp., *Somethus* sp., and *Walesbolus* sp.). Other taxa are being monitored, and the results will be reported. However, the available responses are sufficiently documented to illustrate the significance of experimental design.

Briefly, the amphipod population has been reduced in both abundance and range in the treatments relative to the controls. The scorpion population has not responded to the treatment. The frog went locally extinct in the treated plots, and the population of the scorpion has increased in

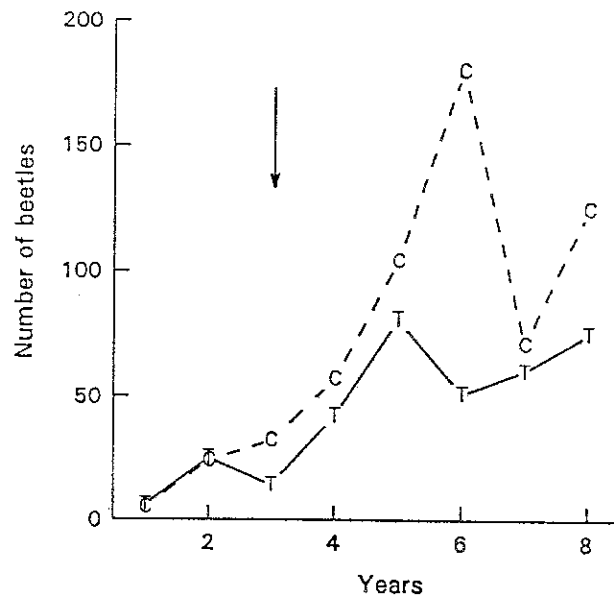


Figure 11.3 The number of *Notonomus respiciens* individuals caught in pitfall traps in the treatments (T) and the controls (C). Overall, the number in the treatments increased, but as a proportion of the total it, in fact, decreased. The arrow marks the treatment time

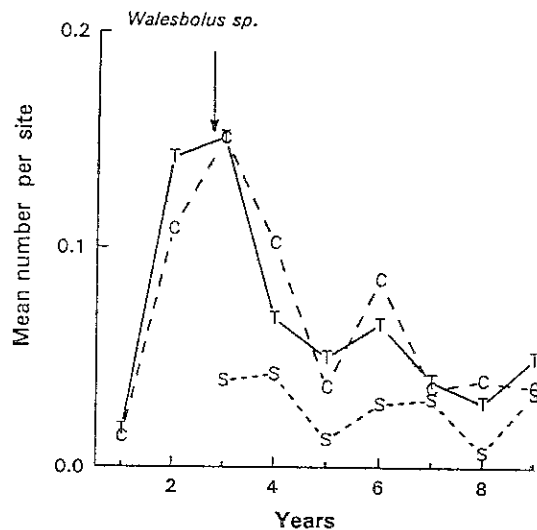


Figure 11.4 Mean numbers of the millipede, *Walesbolus sp.*, caught in pitfall traps over nine years in treatments (T), controls (C), and the 'sea' (S) – the cleared area between forest fragments. The number declined in the treatments, but it also declined in the controls, so the decline in the treatments cannot be interpreted as a treatment effect.

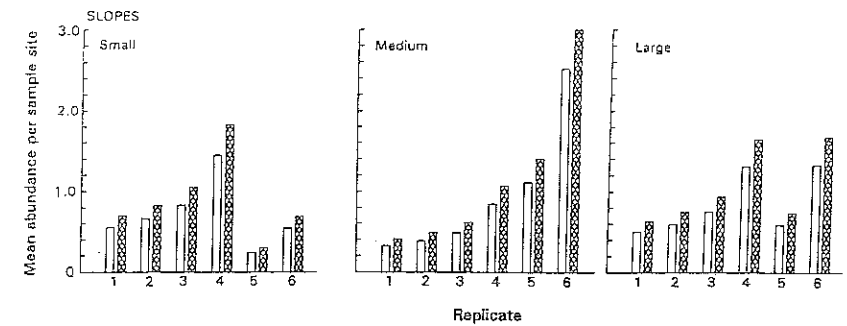


Figure 11.5 Mean abundance of the scorpion *Cercophonius squama* on slopes before (open bars) and after (hatched bars) the fragmentation treatment. Abundances were estimated from a statistical model incorporating the effects of fragment size, treatment versus control, pre- and post-treatment, and replicate. The residual mean deviance was 1.63. See Margules *et al.* (1994) for a full description of the model

In an analysis of pre-treatment data to test whether different treatments and levels might be significant before treatment (e.g. a sampling artifact), Margules (1992) found no differences in the numbers of *Notonomus* spp. among fragment sizes, inner and outer zones, or slopes and drainage lines. However, the block stratum – the between-replicate level – accounted for nearly 42% of the variation in numbers. There were small populations of these species in replicates 4 and 5.

Conversely, there are more scorpions in replicate four than any other treatment replicates. Figure 11.6 is a plot of scorpion abundance in replicate 4 only, post treatment. Without the other treatment replicates, it might have been concluded that scorpions favored small habitat remnants because there are more of them in the small remnant of replicate 4. Replicate 4 is clearly distinct from the other replicates, and within replicate 4, the small and large remnants have larger populations than the medium remnant. These two remnants are adjacent (Figure 11.1), suggesting that local spatial patterns may have influenced the population levels recorded in this case.

**Fewer treatment levels**

Figures 11.7 and 11.8 illustrate the results that would have been obtained for the beetle *Eurylychnus blagravei* and the scorpion *C. squama*, if only one fragment size, in this case the medium size, had been used.

*E. blagravei* was found to be more abundant in habitat fragments post treatment, largely due to the numbers in the small and large fragments. If only medium fragments had been used, it may well have been concluded that fragmentation did not affect populations of this species. Conversely, the conclusion that habitat fragmentation did not affect populations of *C. squama* may not have been reached if only medium fragments had been used because

the treatments, while three others have decreased, and two show no response. Populations of two millipedes increased dramatically in the treatments, while one showed no response.

These results are incorporated in the figures below, which also show the results that might have been obtained if aspects of the experimental design had been different. Some genuine responses may not have been detected, or they may have been misinterpreted.

## RELAXING THE DESIGN

### No controls

The control plots have been crucial to interpreting experimental results so far. In a number of cases, opposite conclusions may well have been drawn without controls. For example, Figure 11.2 shows that without controls, we would almost certainly have concluded that habitat fragmentation favors amphipods. There are many more amphipods now in the forest fragments than there were before the fragmentation treatment. However, relative to the controls, the number has declined sharply. Further analysis of the data from year seven showed that large numbers of amphipods were mainly found in a small number of inner drainage line sites in the large remnants. In the continuous forest, there has been an overall large increase in the abundance of amphipods, which may be part of some longer term trend that is not yet apparent. This increase has not been matched in the forest fragments, where the relative range and abundance of amphipods have declined (Margules *et al.*, 1994).

The same result was found with the carabid beetle *Notonomus resplendens* (Figure 11.3). This species has also declined in the treatments relative to the controls, but without controls the absolute increase in treatments would have been the only data available, leading perhaps to the wrong conclusion.

Similarly, without controls, we may have concluded that habitat fragmentation reduced the abundance of the millipede *Walesbolus* sp. (Figure 11.4). However, the population of this species has declined throughout the experiment, in the controls as well as the treatments, so the decline cannot be ascribed to habitat fragmentation.

Without controls, we would probably have concluded that there was a treatment effect on the abundance of the scorpion *C. squama* (Figure 11.5). There were more scorpions post treatment, but because the controls registered the same small increase post treatment, the change cannot be considered a treatment effect.

### Less replication

Forests are spatially heterogeneous. There is no reason to suppose that any one part of a forest will be just the same as any other part. Replication in sampling, and especially monitoring, is therefore necessary to take this spatial heterogeneity into account.

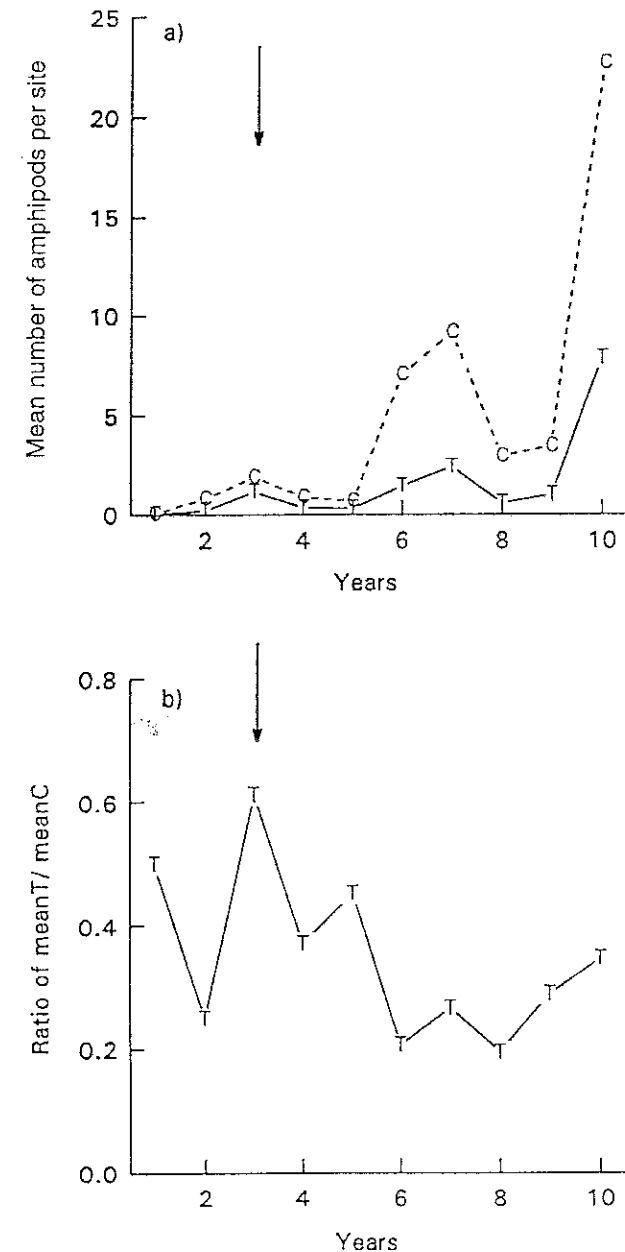


Figure 11.2 Amphipod numbers over 10 years, from 1985 to 1995. Shown are (a) mean number of animals caught in pitfall traps in the controls (C) and treatments (T), and (b) the same figures expressed as the ratio of the number in the treatments compared to the controls. Note that the proportion in the treatments declined markedly. The arrow marks the treatment time.

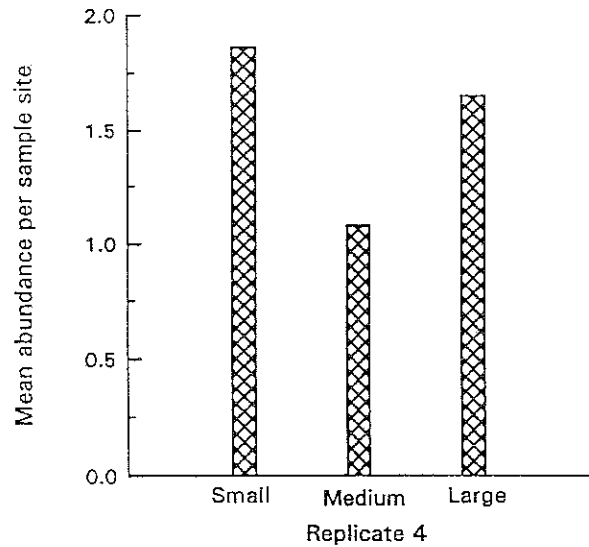


Figure 11.6 An extract from Figure 11.5 showing estimated abundances of *Cercophonius squama* in the three different size fragments of replicate 4, post-treatment. The indication from this result is that scorpions favor small forest fragments. On the contrary, the inclusion of the other replicates (Figure 11.5) shows that there was no treatment effect on this species after six years (Margules *et al.*, 1994)

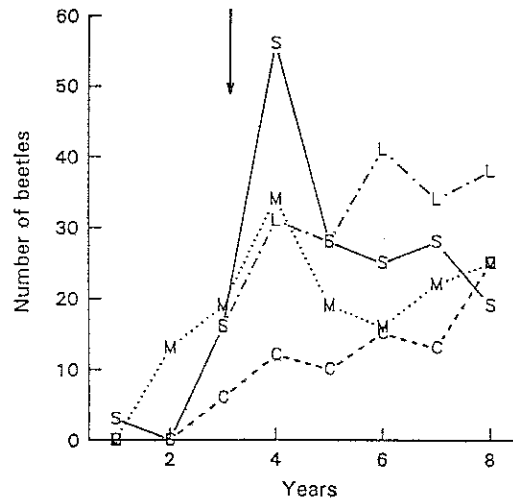


Figure 11.7 The number of *Eurylychnus blagravei* beetles caught in pitfall traps over eight years in the different size fragments (S = small, M = medium, L = large) and in the controls (C). Overall, there were more of these beetles in the forest fragments after fragmentation than before. If only the medium fragments had been compared to the controls, there may have been no significant difference. The arrow marks the treatment time

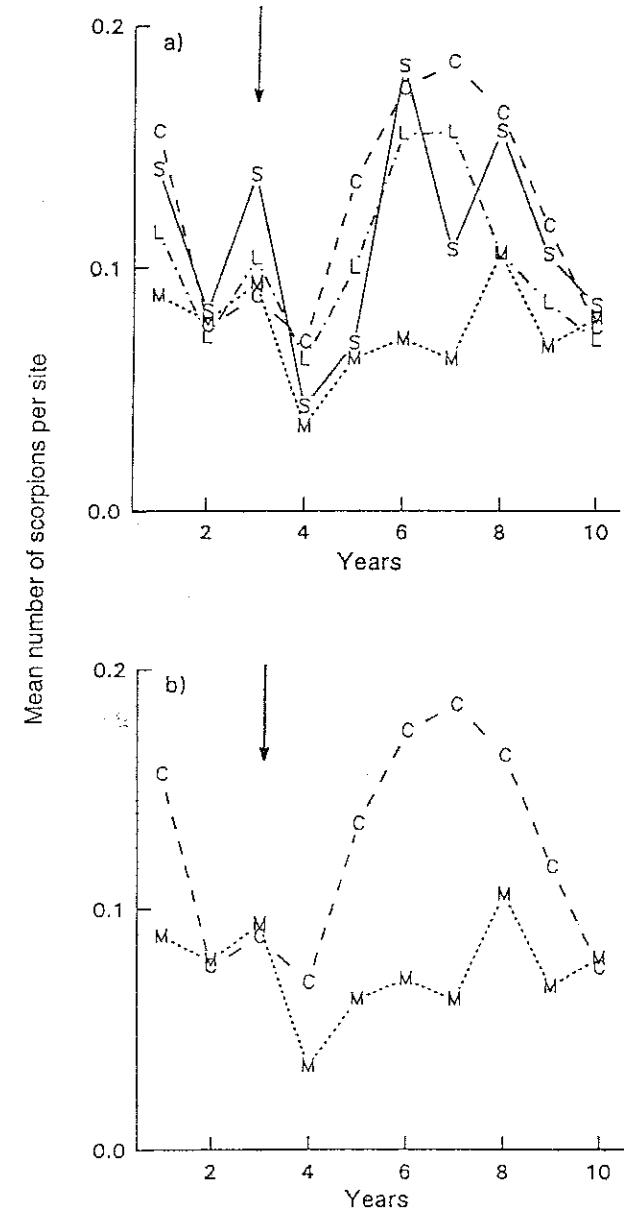


Figure 11.8 The mean number of the scorpion *Cercophonius squama* recorded in pitfall traps in the different size fragments (S = small, M = medium, L = large) and in the controls (C) over 10 years. (These are the raw data used in the model shown in Figure 11.5) In this case, adoption of only medium size remnants may well have led to the conclusion that forest fragmentation reduced scorpion abundance when, in fact, there was no effect. The arrow marks the treatment time

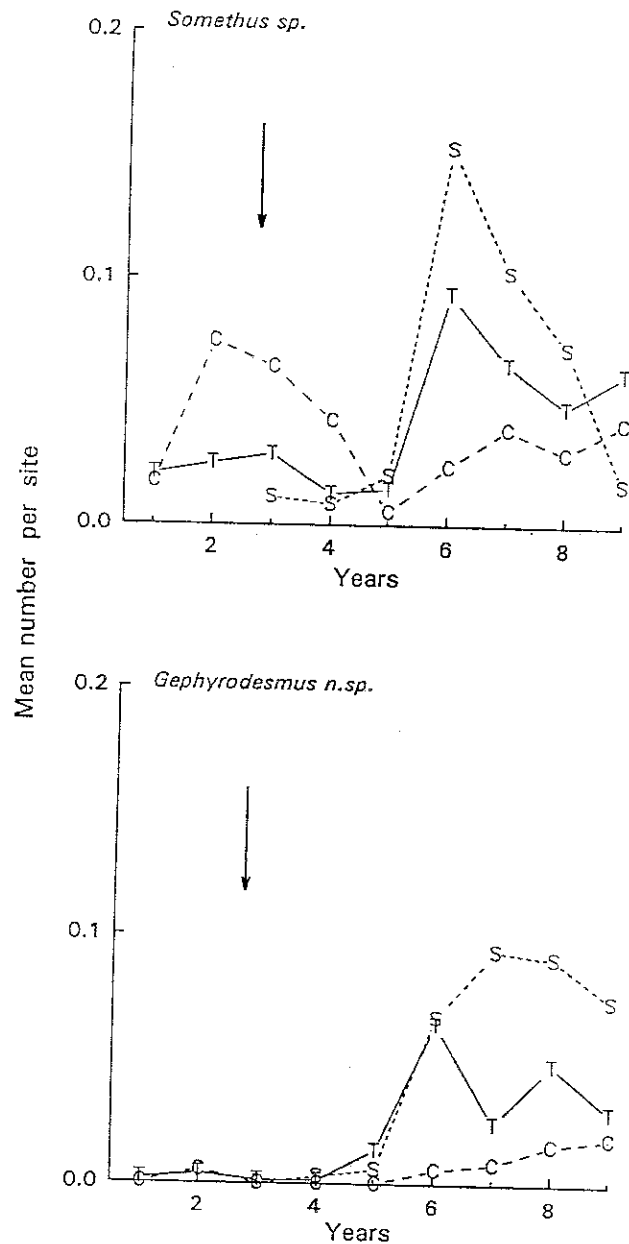


Figure 11.10 Mean numbers of two millipedes, *Somethus* sp. and *Gephyrodesmus* sp., over nine years in the treatments (T), controls (C), and 'sea' (S) – the cleared area between forest fragments. Both species increased dramatically in abundance following forest fragmentation, but if the experiment had not proceeded beyond the seventh year, the trend back to pre-treatment numbers that has become apparent would not have been detected. The arrow marks the treatment time

in relation to testing habitat fragmentation *per se*, it is pseudo-replicated (Hurlbert, 1984). There is no guarantee that the results will be applicable at another location. On the other hand, there is replication of the size treatment. Plots were selected, and then the size treatment was allocated randomly to those plots. There are degrees of freedom available for testing differences due to fragment size; the main difficulty is the lack of interspersed treatments and controls.

Monitoring programs are essential for the long-term management of biodiversity. Unfortunately, ecological processes operate over longer time-scales than do most funding agencies, an important drawback in properly operating monitoring programs that are expensive in time and resources. While it is customary to study ecology over short time-frames and with limited resources (the alternative is often to do nothing), the limitations imposed by such constraints must be recognized – and made explicit.

Suggestions have been made to take advantage of so-called 'natural' experiments – natural catastrophes such as floods, cyclones, fires, etc – and 'accidental' experiments (e.g. Pimm, 1986) – the impacts of human activities such as harvesting, fertilizing, land clearing, etc. – to study ecological processes and the population dynamics of species. Though valuable lessons can certainly be learned from them, they should never be seen as substitutes for real experiments and associated long-term monitoring programs. Natural or accidental experiments meet none of the requirements listed in the introduction. Most critically, there is no control, no replication, and no knowledge of pre-treatment conditions.

The careful design of monitoring programs, especially the often neglected spatial design, will considerably improve the quality of the conclusions that can be drawn and, hence, the reliability of management options that are recommended.

#### ACKNOWLEDGMENTS

John Lawrence maintains the beetle collection and identified the species analyzed here. Geoff Baker identified the millipedes. George Milkovits provided valuable advice and technical support.

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### Less time

If the experiment had continued for only six or seven years, it would have been correctly concluded that *C. signifera* had gone locally extinct due to habitat fragmentation, even though the species recolonized in the eighth year (Figure 11.9). Interestingly, if sampling had been at very long intervals, say 10 years, this local extinction and recolonization would have been missed.

Similarly, if the experiment had gone for only seven years, the trend back towards near pre-treatment numbers now being seen in the millipedes *Somethus* sp. and *Gephyrodesmus* sp. would not have been detected (Figure 11.10). The importance of a reasonable time series has been emphasized many times. Recently, Dodd *et al.* (1995) detected population abundance changes over a 60-year period that would not have been predicted with data from shorter time periods.

### No environmental stratification

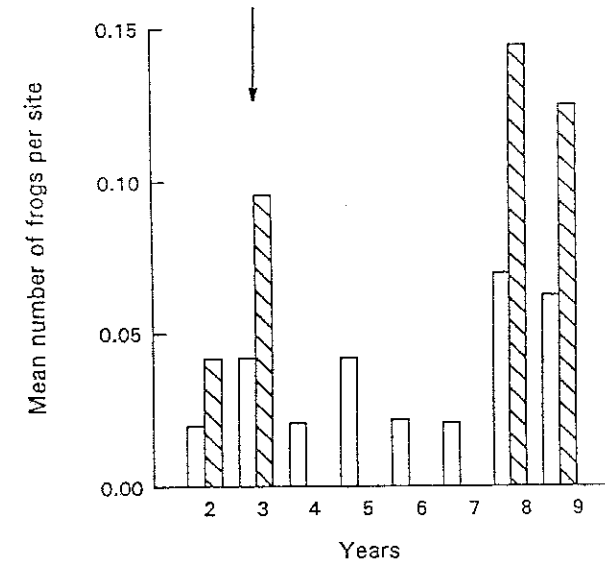
Internal stratification of each plot or fragment into slopes or drainage lines was necessary to capture the habitat preferences of more specialized species and facilitate analyses of the responses of less abundant species. Without environmental stratification, species occurring only or predominantly in drainage lines or on slopes may not have been sampled at all, or may have been sampled in numbers too low for adequate analyses to be performed. Data on the response of the frog *C. signifera* (Figure 11.9) are from inner drainage lines in summers. It proved easier to detect a response by focusing on that particular stratum.

There is a much lower probability of finding scorpions in drainage lines than on slopes (Margules *et al.*, 1994). Analysis of the population level response of scorpions to habitat fragmentation (Figure 11.5) was made simpler by eliminating one potential source of unexplained variation; i.e. low numbers in drainage lines.

## DISCUSSION

It is extremely difficult to design satisfactory field experiments, which is how all monitoring programs can be classified. Statistical correctness is all but impossible to attain because of both the presence of many uncontrollable variables and the enormous practical problems associated with gathering samples from the field. However, these are not sufficient reasons for ignoring statistical rigor and, in fact, are motivations for designing monitoring activities, keeping the goal of the exercise clearly in mind.

The Wog Wog experiment was established to test the responses of populations to fragmentation of their habitat. This required a monitoring program designed specifically for that purpose. The experiment satisfies many, although not all, of the design features identified as desirable in the introduction, and it has allowed



**Figure 11.9** Abundance of the frog *Crinia signifera* during summers in treatments (hatched bars) versus controls (open bars). If the experiment had not continued past the seventh year, it would have been concluded that this species was locally extinct in the forest fragments. In fact, it recolonized in the eighth year. The arrow marks the treatment time

statistical testing of the responses of populations of at least eight species to date, as described above.

Pre-treatment monitoring was needed to establish the underlying (natural or untreated) spatial patterns in distribution and abundance. It also helped identify some temporal patterns, although the period was too short to provide detailed information on fluctuations over time. For this purpose, only the controls are available to measure such effects, and the power of the experiment is reduced.

Environmental stratification into slopes and drainage lines is essential for examining vegetation (Austin and Nicholls, 1987) and was also shown to have a strong influence on the probability of finding scorpions and amphipods (Margules *et al.*, 1994). In this case, separate analyses of those two strata improved the predictive power of the results. No doubt analyses of many other species, still to come, will be similarly improved.

The need for a long time period in monitoring studies was demonstrated for populations of several species, and it is unlikely that the 10 years elapsed so far is sufficient to separate from treatment effects all of the impacts on population size that stem from factors such as demographic and climatic stochasticity (see, e.g. Dodd *et al.*, 1995).

The most serious weakness of the Wog Wog habitat fragmentation experiment is its restriction to one geographic location. It is not replicated elsewhere. Thus,

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## CHAPTER 12

### LARGE-SCALE PATTERNS OF SEED DISPERSAL

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#### INTRODUCTION

The dispersal of seeds is an important stage in the life-cycle of plants. The ability of plants to reproduce successfully depends in part on dispersal of their seeds into locations that offer greater chances of germination and survival. The distance and location of dispersal can have significant impact on the survival of the seed (Howe and Smallwood, 1982). In addition, the distribution of species across large geographic ranges is affected by its dispersal characteristics (Gentry, 1983; Tilman, 1994; Whittaker and Jones, 1994). The mode of dispersal – i.e. biotic such as by animals or abiotic such as by wind, water, or adhesion – can influence a species ability to disperse its seeds effectively (Ridley, 1930; van der Pijl, 1982). For example, species with biotic dispersal modes may be limited by the occurrence and densities of suitable animals (Gentry, 1983). The dispersal mode of a species is not likely to change over short time scales and it can be highly influential in determining distribution and success of a species (Howe and Primack, 1975; Dale, 1988).

To date, much of the research on seed dispersal has emphasized the relationships of different plant species and their dispersal agents (see papers in Estrada and Fleming, 1986 and Fleming and Estrada, 1993). Other studies have focused on issues relating to neotropical forest dynamics, where the role of tree-fall gaps and gap regeneration properties have been explored (Levey, 1988a; Denslow and Gomez Diaz, 1990). In these forests, bats and wind are believed to play an important role in dispersing small-seeded plants, especially into newly created gaps, while late-successional species and those of the mature understory and canopy, with larger seeds, are primarily dispersed by biotic agents (Schupp *et al.*, 1989). This work is often limited to investigation of specific dispersers such as bats (Fleming *et al.*, 1985; Gorchoy *et al.*, 1993), birds (McClanahan and Wolfe, 1993; Robinson and Handel, 1993; De Foresta *et al.*, 1984), and other agents (Charles-Dominique, 1986; Guevara *et al.*, 1986; Lawton and Putz, 1988; Guevara *et al.*, 1992; Hiroki and Ichino, 1993).

Only a few studies, primarily in the neotropics, have addressed multiple dispersal modes and the relative role of abiotic and biotic dispersers (Gentry, 1982; Foster *et al.*, 1986; Roth, 1986; Willson and Crome, 1989; Willson *et al.*, 1990). Fewer still have included questions relating to succession following disturbance (Tidemann *et al.* 1990, Hickey 1994, Whittaker and Jones 1994).