

Occupancy-abundance models for predicting densities of three leaf beetles damaging the multipurpose tree *Sesbania sesban* in eastern and southern Africa

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Abstract

Mesoplatys ochroptera Stål, *Exosoma* and *Oothea* spp. seriously damage *Sesbania sesban* (L.) Merrill, a multipurpose leguminous tree widely used in tropical agroforestry. This is discouraging farmers from expanding the planting of *Sesbania* in various agroforestry systems in eastern and south-central Africa. Rapid methods are needed for estimation of population densities of these beetles for decision-making in pest management. A study was conducted with the objectives of determining the existence of any positive relationship between the occupancy and abundance of *Mesoplatys*, *Exosoma* and *Oothea* and determining the model that best predicts abundance from occupancy for rapid estimation of population densities. The Poisson model assuming spatial randomness, the negative binomial distribution (NBD) model assuming spatial aggregation, the Nachman model without any distribution assumption, and a General model incorporating spatial variance-abundance and occupancy-abundance relationships were fitted to data on adult *M. ochroptera*, *Exosoma* and *Oothea* from western Kenya, southern Malawi and eastern Zambia. Very strong variance to abundance relationships were observed in the spatial pattern of all three beetles. The occupancy-abundance relationships were also positive and strong in all beetles. The occupancy and abundance predicted by the four models were closest to the observed at lower densities compared with higher beetle densities. At higher population densities, the NBD and the General model gave better fit for *M. ochroptera* and *Exosoma*. For *Oothea* populations, the Poisson and NBD models gave better fit at higher population densities. The relationships established here can be used as guide to estimate beetle densities for decision-making in pest management.

Keywords: binomial sampling, *Exosoma*, *Mesoplatys*, *Oothea*, power law

Introduction

Sesbania, *Sesbania sesban* (L.) Merrill, is a multipurpose leguminous tree widely used in the tropics for improvement of soil fertility, soil conservation and as a source of animal fodder and fuel wood (Evans & Rotar, 1987; Kwesiga *et al.*, 1999). Among the legumes widely used in agroforestry practices in eastern and southern Africa, *Sesbania* is the only species indigenous to the region. With its centre of origin being in Africa, *Sesbania* grows naturally in most parts of eastern and

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southern Africa (Ndungu & Boland, 1994). Hence, sesbania has more appeal considering the potential for invasiveness of the exotic species. However, damage by *Mesoplatys ochroptera* Stål, *Exosoma* and *Oothecca* spp. (mainly *Oothecca bennigseni* Weise) (Coleoptera: Chrysomelidae) is discouraging farmers from planting sesbania (Sileshi *et al.*, 2000). *Mesoplatys ochroptera* has been widely reported as a serious pest of sesbania in Ethiopia, Kenya, Malawi, Mozambique, Tanzania, Zambia and Uganda (Mchowa & Ngugi, 1994; Sileshi *et al.*, 2000, 2002, 2003 and references in Sileshi *et al.*, 2003), while *Exosoma* sp. has been reported so far only from Malawi and Zambia (Mchowa & Ngugi, 1994; Sileshi *et al.*, 2000). In addition to sesbania, *Oothecca* species also attack common bean (*Phaseolus vulgaris* L.), cowpea (*Vigna unguiculata* L.) and Bambara groundnut (*Vigna subterranea* (L.) Verdc) in eastern and southern Africa (Karel, 1989; Allen *et al.*, 1996). *Oothecca* species are of major concern to farmers in Zambia (Sithanatham *et al.*, 1989), Malawi (Ross, 1998) and Tanzania (Karel, 1989) as they can wipe out the whole crop of beans. Recently, *Oothecca* species have been reported as serious defoliators of sesbania in Zambia and Malawi (Sileshi *et al.*, 2000).

The design of integrated management for these beetles is difficult because little is known on their population dynamics in most of the countries where sesbania is grown in agroforestry. Sileshi *et al.* (2002) studied the spatial distribution of *M. ochroptera* and developed enumerative sampling plans suitable for population dynamics studies in southern Africa. However, more rapid methods are needed for decision-making in pest management, especially for *Exosoma* and *Oothecca* species. The present study investigates suitability of models that relate patch occupancy to abundance for predicting densities of leaf beetles.

Interest in patch occupancy, at least in a population monitoring context, is often motivated by its likely relationship to abundance (Royle & Nichols, 2003; Royle *et al.*, 2005). Recently, this relationship has attracted considerable theoretical and practical attention in metapopulation biology and in macroecology (Hartley, 1998; Strayer, 1999; Gaston *et al.*, 2000; He *et al.*, 2002; He & Gaston, 2003; Warren *et al.*, 2003; Royle *et al.*, 2005). This is based on the observation that the proportion of areas occupied by a species (p , its incidence or probability of occurrence in a sample) increases with its mean abundance (μ) among those areas, and again that this is manifest from micro- to macro-spatial scales both for a given species at different times or in different regions and for different species across the same set of areas (Hartley, 1998; He & Gaston, 2003). This relationship is so widespread that it has been purported as one of the few general rules of ecology (Hartley, 1998). Occupancy-abundance models are particularly appealing in pest management because they yield inferences about the status of populations based only on the presence or absence of individuals, data that can be relatively easily collected. Therefore, the objectives of the present study were to determine: (i) whether any positive relationship exists between the occupancy and local abundance of the three beetle species; and (ii) the model that best predicts abundance from the occupancy of each species.

Materials and methods

The sources of data

The first dataset came from studies conducted in southern Malawi and eastern Zambia described in detail

in earlier studies by Sileshi *et al.* (2000, 2002, 2003). Incidence and abundance data were collected from various agroforestry practices involving sesbania in southern Malawi and eastern Zambia (referred to as southern Africa hereafter) between 1997 and 2001. Sampling was conducted at the Msekera Research Station in eastern Zambia and Makoka research station in southern Malawi as well as on farmers' fields. From each field (referred to as a plot hereafter), 30 randomly selected seedlings were examined and the number of adults, eggs and larvae of *M. ochroptera*, *Exosoma* and *Oothecca* were recorded. All plots were sampled approximately 40 to 60 days after transplanting in the field.

The second dataset came from studies in western Kenya. *Mesoplatys ochroptera* incidence and abundance were monitored in two experiments established during 1999–2000 and 2000–2001. The experimental sites were Dudi and Khumusalaba in Butere district, Mutumbu in Siaya district, and Lela in Kisumu district of western Kenya. Abundance of *M. ochroptera* was monitored on 15 plants at monthly intervals from June to December. During early growth stages, the whole tree was used as a sampling unit, and later as the trees grew taller counting was restricted to a height of 2 m from the ground. Adult *M. ochroptera* was counted and presence or absence were recorded from each plant.

The modelling approach and assumptions

In the present study, abundance is defined as the mean density of individuals in the habitat patches (entire plants) in which a species is present, and occupancy as the proportion of the total number of patches that are occupied. The fundamental relationship between abundance and occupancy has been elaborated by Royle *et al.* (2005). Specifically, let N_i be the abundance of a species in a set of spatial locations $i = 1, 2, \dots, R$. If the N_i are viewed as realizations of a random variable with density $g(N; \theta)$, then occurrence probability (patch occupancy) is simply $Pr(N > 0; \theta)$. Thus, a characterization of the abundance distribution yields a characterization of occupancy (Royle *et al.*, 2005).

The first occupancy-abundance model (model 1) was derived from the Poisson distribution by assuming spatial randomness and mutual independence in the distribution of individuals of the beetle species. This is based on the observation that both plant and animal populations agree substantially with the Poisson distribution at low densities (Bliss & Fisher, 1953; Onsager, 1981). For this reason, it is a standard null model for the distribution of animals in many ecological studies (Royle *et al.*, 2005). Under the Poisson assumption, the proportion (p) of sampling units with at least one individual of each species is given by:

$$p = 1 - e^{-\mu} \quad (1)$$

where p is also the probability of occurrence (or occupancy) of a species in a sampling unit, and μ is the mean number of individuals per plant.

Since numerous insect species typically occur in aggregated patterns, the assumption of mutual independence (model 1) is open to question. Anscombe (1949) pointed out that the Poisson is but a special case of a more general form of distribution, the negative binomial distribution (NBD) described by two parameters, μ and k . Hence, for species that show moderate to highly aggregated spatial pattern, the

occupancy-abundance model can be derived from the NBD (Wilson & Room, 1983; Kuno, 1986; Wright, 1991; He & Gaston, 2002; Royle *et al.*, 2005) as an extension of the Poisson. Model 2 assumes spatial aggregation, and the proportion (p) of sampling units with at least one individual of each species is given by:

$$p = 1 - \left(1 + \frac{\mu}{k}\right)^{-k} \quad (2)$$

where k is a spatial aggregation parameter. Although parameter k in the NBD has originally been defined as non-negative, recently it has been shown to assume negative value (Kuno, 1986; He & Gaston, 2003). Hence, when $k < -\mu$, model 2 is derived from the positive binomial distribution that describes spatial regularity, and when $k > 0$, it is derived from the negative binomial distribution for spatial aggregation (He & Gaston, 2003). If the value of k is infinitely large, the NBD reduces to the Poisson distribution. The parameter k was estimated by the maximum likelihood method using the GENMOD procedure of SAS (SAS, 2003).

Model 3 has no distribution assumption, and it is based on Nachman's empirical model (Nachman, 1981), which has been traditionally used in economic entomology for estimating pest density μ from p . Here, the proportion of sampling units with at least one individual is given by:

$$p = 1 - e^{(-\alpha\mu^\beta)} \quad (3)$$

where α is a positive parameter, and β is a scale parameter that determines the shape and curvature of the p versus μ curve. The parameters α and β were estimated by ordinary least square regression of the log of the sample means (m) on the proportion (p) of non-infested plants as:

$$\log m = \alpha + \beta \log \left(\ln \left(\frac{1}{1-p} \right) \right) \quad (4)$$

Model 4 (hereafter called the 'General' model) emerges as a result of unification of two general phenomenological models, namely, the variance-mean relationship described by Taylor's power law (Taylor, 1961) and occupancy-abundance models (He & Gaston, 2003). The relationship emphasized by He & Gaston's (2003) emerges as a natural consequence of the fact that abundance, occupancy, and variance in abundance are completely specified by the species abundance distribution (Royle *et al.*, 2005). In model 4, the proportion (p) of sampling units with at least one individual of each species is given by:

$$p = 1 - \left(\frac{\mu}{\sigma^2} \right)^{\frac{\mu}{\sigma^2 - \mu}} \quad (5)$$

where $\sigma^2 \neq \mu$ but can infinitely approach μ , resulting in $p = 1 - e^{-\mu}$ which is the occupancy for the Poisson distribution (equation 1). The variances in model 4 are derived from the mean using Taylor's power law given by:

$$\sigma^2 = a\mu^b \quad (6)$$

where a and b are parameters to be estimated via linear regression of the log-transformed sample variances (s^2) on log-transformed sample means (m).

The occupancy-abundance data on adult *M. ochroptera*, *Exosoma* and *Oothea* were fitted to models 1–4. Once such a relationship was established, the estimate of μ was obtained

from occupancy using equations 7, 8 and 9 below for the Poisson, NBD and Nachman models:

$$\bar{\mu} = -\ln(1-p) \quad (7)$$

$$\bar{\mu} = k((1-p)^{-1/k} - 1) \quad (8)$$

$$\bar{\mu} = \left(-\frac{\ln(1-p)}{\alpha} \right)^{1/\beta} \quad (9)$$

The final criterion of the applicability of the occupancy-abundance models was to compare the expected values (fitted occupancy, p_f or fitted mean m_f) from models 1–4 with the observed occupancy (p_o) or mean (m_o). Here we are more interested in the relative performance of the models than a rigorous statistical test. The agreement between the expected and observed data was tested using linear regression of the fitted values against the observed (Wilson *et al.*, 1983; He & Gaston, 2003). The regression was forced to pass through the origin, and when an estimate of the slope was closer to unity with 90% or more explained variation ($r^2 > 0.90$), the model fit was judged as adequate. The sum of absolute differences ($|\Delta p|$) between observed occupancy (p_o) and the fitted occupancy (p_f) as well as the sum of differences ($|\Delta m|$) between observed abundance (m_o) and abundance predicted (m_f) by a specified model were also used as an approximate test of goodness-of-fit as suggested by He *et al.* (2002). The sum of absolute differences ($|\Delta p|$) was derived as:

$$\sum |\Delta p| = \sum_{i=1}^s |p_o - p_f| \text{ or } \sum |\Delta m| = \sum_{i=1}^s |m_o - m_f| \quad (10)$$

Results

Strong and positive relationships ($r^2 > 0.90$) were found between the spatial variance and abundance of the beetle species except for *Oothea* (table 1 and fig. 1). The values of Taylor's aggregation parameter (b) were generally smaller for *Oothea* compared with *Exosoma* sp. and *M. ochroptera*. The occupancy-abundance relationships were also positive in all beetles (tables 2 and 3; figs 2–5). Both abundance and occupancy of *M. ochroptera* were much higher compared with those of *Exosoma* and *Oothea* (figs 2–5). The observed occupancy for *Exosoma* was less than 80% of the sampling units, while occupancy of *Oothea* never exceeded 70% of the sampling units in any one sample. While abundance of *M. ochroptera* could exceed 10 adults per plant, that of *Oothea* never exceeded one adult per plant in any one sample. Parameter estimates used in predicting occupancy from abundance are presented in table 1. The respective parameter estimates of Taylor's power law and the Nachman model used in the General and Nachman occupancy-abundance models were judged adequate since the explained variation ($r^2 > 0.78$) was sufficiently high. Regression of the expected occupancy and abundance against the observed occupancy and abundance, respectively, resulted in over 90% explained variation under the assumptions of the Poisson, NBD and General model for the three beetles except for *M. ochroptera* in western Kenya (table 2). The variation explained by regression of the expected abundance against the observed under the assumptions of the Nachman model was very low for *Oothea*.

Figures 2 and 3 show the observed occupancy of *M. ochroptera* and that predicted from its abundance using the four models in western Kenya and southern Africa,

Table 1. Parameter estimates of Taylor's power law, parameter k of the negative binomial distribution (NBD) and Nachman's model for the occupancy-abundance relationship describing intraspecific spatial patterns of adult *Mesoplatys ochroptera*, *Exosoma* and *Oothea* in sesbania in southern Africa and western Kenya.

Species	Sites and number of samples (n)	Model parameters	Taylor's power law	Parameter k of NBD	Nachman
<i>Mesoplatys</i>	Southern Africa $n = 149$	Intercept (a)	0.29 ± 0.02	–	0.50 ± 0.07
		Slope (b)	1.19 ± 0.03	2.90 ± 0.17	1.10 ± 0.10
		r^2	0.91	1.01*	0.78
	Western Kenya $n = 94$	Intercept (a)	0.54 ± 0.03	–	1.05 ± 0.09
		Slope (b)	1.41 ± 0.05	0.45 ± 0.10	1.21 ± 0.06
		r^2	0.91	0.94*	0.82
<i>Exosoma</i>	Southern Africa $n = 98$	Intercept (a)	0.34 ± 0.03	–	0.71 ± 0.12
		Slope (b)	1.33 ± 0.03	1.37 ± 0.40	1.27 ± 0.05
		r^2	0.95	0.67*	0.85
<i>Oothea</i>	Southern Africa $n = 63$	Intercept (a)	-0.03 ± 0.05	–	0.12 ± 0.09
		Slope (b)	0.96 ± 0.05	-1.67 ± 1.51	0.95 ± 0.04
		r^2	0.88	0.11*	0.91

* Deviance divided by the degrees of freedom.

respectively. The occupancy predicted by all four models was closer to the observed at low densities (<2 beetles per plant) of *M. ochroptera* (figs 2 and 3), while at high densities (>8 beetles per plant) the proportion of infested plants saturated, yielding little information about abundance. As indicated by values of the regression coefficients and absolute differences, the occupancy and abundance predicted by the NBD and General models showed a close fit to the predicted occupancy (table 2) and abundance (table 3), respectively. The Poisson overestimated occupancy and underestimated abundance of *M. ochroptera* at both sites (figs 2 and 3). The Nachman model overestimated occupancy and underestimated abundance from the western Kenya data.

Figure 4 shows the occupancy of *Exosoma* predicted from its abundance and vice versa using the four models. At low densities of *Exosoma* (<2 beetles per plant), either the occupancy or abundance predicted by all the models was closer to the observed, while at higher densities (>2 beetles per plant) there were huge disparities (fig. 4). From values of the regression coefficients and absolute differences it can be seen that the NBD and General models predicted both occupancy and abundance closer to the observed (tables 2 and 3). The Poisson and Nachman models overestimated occupancy and underestimated abundance of *Exosoma* (fig. 4).

The occupancy of *Oothea* predicted from its abundance or vice versa using the four models is depicted in fig. 5. *Oothea* was less abundant and hence its occupancy remained low compared with *M. ochroptera* and *Exosoma*. The Poisson, NBD and General models predicted both occupancy and abundance closer to the observed, while the Nachman model either underestimated occupancy or overestimated abundance of *Oothea* (fig. 4; tables 2 and 3).

Discussion

The slopes of the variance-mean relationship were generally smaller for *Oothea* than *M. ochroptera* and *Exosoma*, indicating the possibility of its competition with any two species. Recent analyses have demonstrated that the slope of the variance-mean relationship is a reflection of competitive

interactions among species in a community and species response to environmental and demographic stochasticity (Kilpatrick & Ives, 2003; Marquet *et al.*, 2005). The observed occupancy of *Oothea* was lower than that of *M. ochroptera* and *Exosoma*. This is probably because *Oothea* is displaced by the more common species, which are superior competitors.

The intraspecific occupancy-abundance relationships for *M. ochroptera*, *Exosoma* and *Oothea* are typical of such relationships reported in the literature (Gaston & Curnutt, 1998). *Oothea* was rarer than *M. ochroptera* and *Exosoma* and had lower occupancy, while the most abundant species, *M. ochroptera*, had the highest occupancy. This is also in agreement with reports that rare species not only have restricted distribution but they also occur at low densities where they are found, whereas widespread species tend to be very abundant where they occur (Conrad *et al.*, 2001).

The occupancy predicted by models 1–4 showed agreement with the observed occupancy in all the three beetle species at low densities. However, occupancy yielded little information about abundance at high densities of *M. ochroptera*. The occupancy and abundance predicted by the NBD model showed closer fit to the observed occupancy of *M. ochroptera* and *Exosoma*. This is consistent with our earlier work (Sileshi *et al.*, 2002) showing aggregated spatial distribution of *M. ochroptera*, which could be adequately described by the NBD. The General and Nachman models also gave good fit of the occupancy of *Exosoma* sp. For prediction of both occupancy and abundance of *Oothea*, the Poisson model appears to be the best. Although the NBD model appears to give a good fit to the occupancy of all three species especially at higher densities, its applicability may be limited due to the danger of using a constant k of the NBD. The limitation of a common k as an ecological indicator of aggregation has been indicated by Taylor and co-workers (Taylor *et al.*, 1979; Perry & Taylor, 1986). The high variability of this parameter often obscures the relationship of $1/k$ with population density (Perry & Taylor, 1986). Where the validity of a constant k is questionable, the use of the variances predicted by Taylor's power law in the General model to construct occupancy-abundance relationships is more appealing. This is because the variance-mean

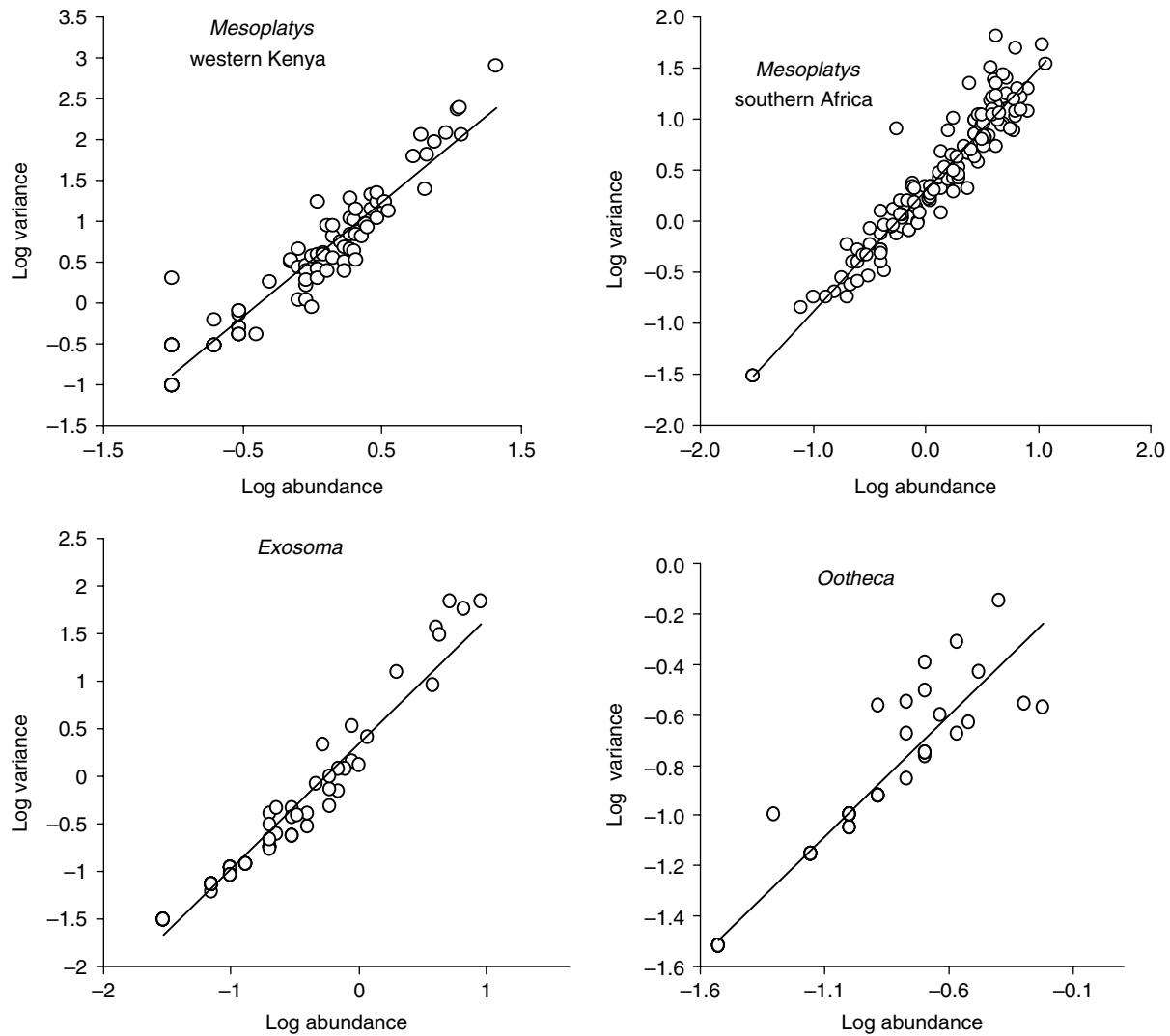


Fig. 1. Relationship between spatial variance and abundance of *Mesoplatys ochroptera*, *Exosoma* and *Oothea* spp. in sesbania in western Kenya and southern Africa.

Table 2. Least square estimates of the explained variation (r^2) for the occupancy-abundance relationship and sum of absolute differences ($|\Delta p|$) between the observed occupancy and occupancy predicted by the four models for adult *Mesoplatys ochroptera*, *Exosoma* and *Oothea* in sesbania in southern Africa and western Kenya.

Criterion	Beetle species	Poisson	NBD	General	Nachman
Explained variation	<i>Mesoplatys</i> southern Africa	0.942	0.960	0.942	0.942
	<i>Mesoplatys</i> western Kenya	0.894	0.953	0.899	0.871
	<i>Exosoma</i> southern Africa	0.980	0.985	0.978	0.981
	<i>Oothea</i> southern Africa	0.993	0.993	0.993	0.983
Slope \pm SE	<i>Mesoplatys</i> southern Africa	0.87 ± 0.02	0.91 ± 0.01	1.43 ± 0.03	2.84 ± 0.05
	<i>Mesoplatys</i> western Kenya	0.75 ± 0.03	0.88 ± 0.02	1.31 ± 0.05	1.98 ± 0.08
	<i>Exosoma</i> southern Africa	0.98 ± 0.01	0.99 ± 0.01	1.66 ± 0.03	3.13 ± 0.05
	<i>Oothea</i> southern Africa	1.00 ± 0.01	0.98 ± 0.01	1.61 ± 0.02	4.11 ± 0.07
Sum of absolute differences ($ \Delta m $)	<i>Mesoplatys</i> southern Africa	19.6	13.5	15.3	17.9
	<i>Mesoplatys</i> western Kenya	17.9	7.0	11.9	18.5
	<i>Exosoma</i> southern Africa	6.3	4.9	10.1	9.2
	<i>Oothea</i> southern Africa	1.2	0.9	5.0	6.6

Table 3. Least square estimates of the explained variation (r^2) for the abundance-occupancy relationship and sum of absolute differences ($|\Delta m|$) between the observed abundance and abundance predicted by the four models for adult *Mesoplatys ochroptera*, *Exosoma* and *Oothea* in sesbania in southern Africa and western Kenya.

Criterion	Beetle species	Poisson	NBD	General	Nachman
Explained variation	<i>Mesoplatys</i> southern Africa	0.829	0.799	0.900	0.883
	<i>Mesoplatys</i> western Kenya	0.625	0.835	0.737	0.542
	<i>Exosoma</i> southern Africa	0.936	0.937	0.942	0.952
	<i>Oothea</i> southern Africa	0.989	0.992	0.990	0.152
Slope \pm SE	<i>Mesoplatys</i> southern Africa	1.33 ± 0.04	0.73 ± 0.03	0.88 ± 0.02	2.14 ± 0.06
	<i>Mesoplatys</i> western Kenya	0.86 ± 0.07	1.09 ± 0.05	0.62 ± 0.04	2.05 ± 0.20
	<i>Exosoma</i> southern Africa	1.04 ± 0.03	0.96 ± 0.03	0.92 ± 0.02	2.22 ± 0.05
	<i>Oothea</i> southern Africa	0.99 ± 0.01	0.99 ± 0.01	2.26 ± 0.03	0.11 ± 0.03
Sum of absolute differences ($ \Delta m $)	<i>Mesoplatys</i> southern Africa	910.6	230.5	139.4	175.1
	<i>Mesoplatys</i> western Kenya	91.3	94.6	71.5	101.8
	<i>Exosoma</i> southern Africa	246.8	31.5	28.7	31.4
	<i>Oothea</i> southern Africa	2.2	1.6	2.3	68.3

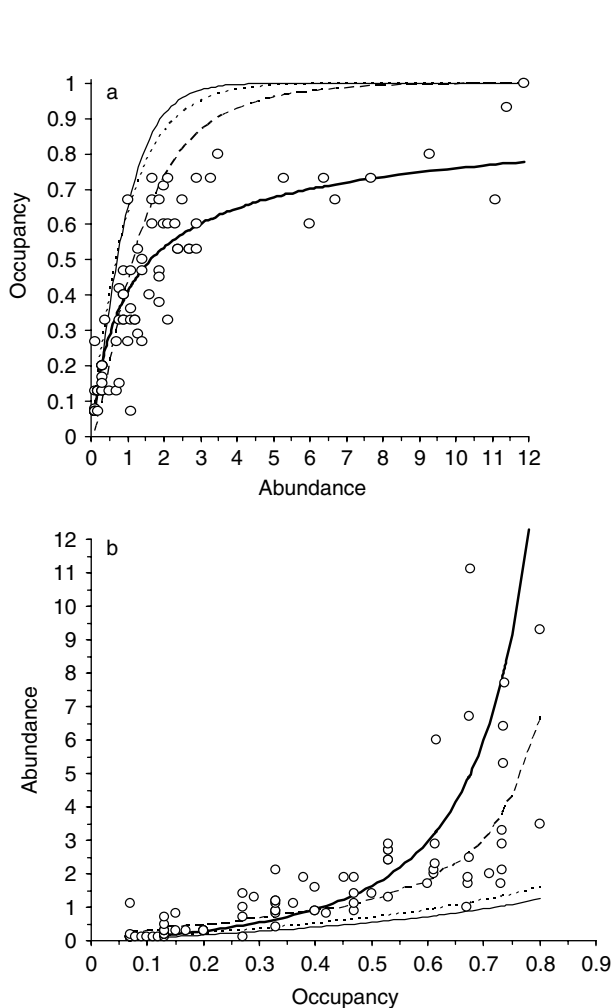


Fig. 2. Observed and predicted occupancy (proportion of plants infested) versus observed abundance (density per plant) (a) and observed abundance and abundance predicted from occupancy (b) of *M. ochroptera* in sesbania in western Kenya (o, observed; ---, General model;, Poisson model; —, negative binomial distribution (NBD) model; —, Nachman model).

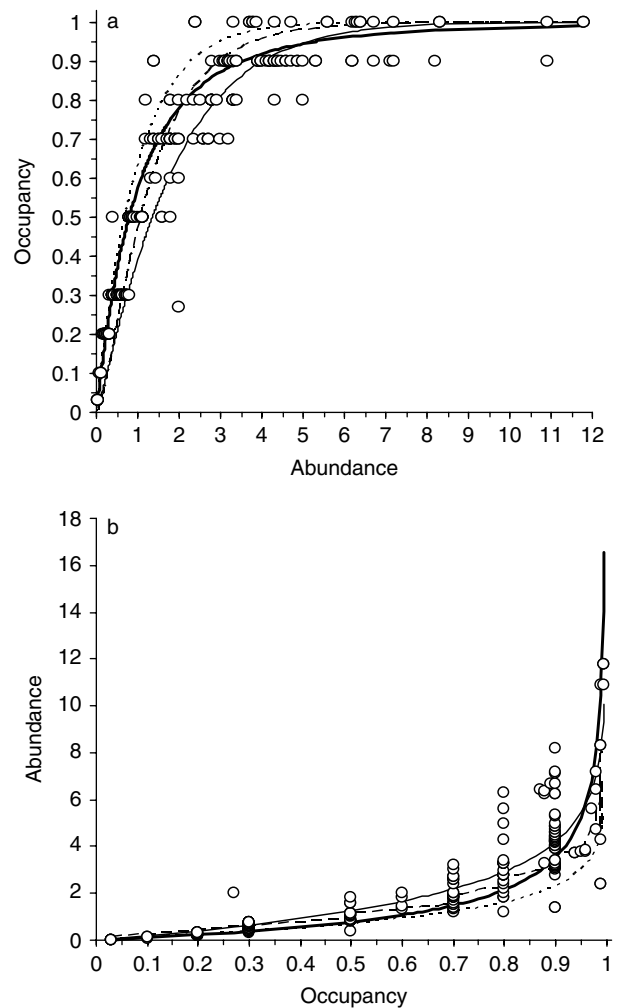


Fig. 3. Observed and predicted occupancy (proportion of plants infested) versus observed abundance (density per plant) (a) and observed abundance and abundance predicted from occupancy (b) of *M. ochroptera* in sesbania in southern Africa (o, observed; ---, General model;, Poisson model; —, negative binomial distribution (NBD) model; —, Nachman model).

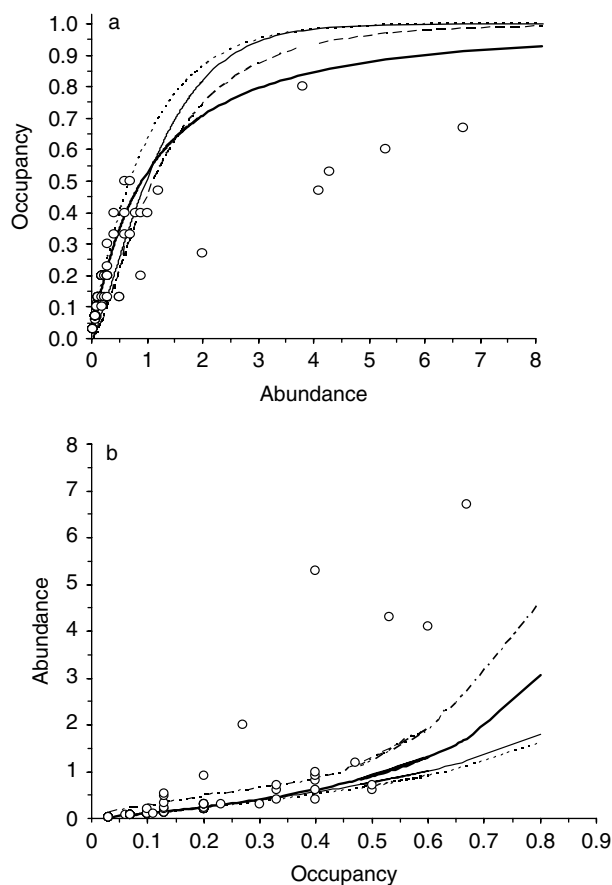


Fig. 4. Observed and predicted occupancy (proportion of plants infested) versus observed abundance (density per plant) (a) and observed abundance and abundance predicted from occupancy (b) of *Exosoma* sp. in sesbania in southern Africa (o, observed; ---, General model;, Poisson model; —, negative binomial distribution (NBD) model; —, Nachman model).

relationship has been very strong (fig. 1; table 1). In addition, recent evidence suggests the universality and scale invariance of power laws (Brown *et al.*, 2002; He & Gaston, 2003; Marquet *et al.*, 2005), which makes them very well suited for the study of ecological systems that show variability at different temporal and spatial scales. Taylor's power law has been established for more than 400 taxa ranging from protozoa to vertebrates (Brown *et al.*, 2002; He & Gaston, 2003; Kilpatrick & Ives, 2003). Variance-mean and occupancy-abundance patterns characterize the spatial distribution of species and share a common currency of abundance. Until recently, there has been little attempt in ecology to explore the connections between the two. He & Gaston (2003) have empirically demonstrated that Taylor's mean-variance relationship and occupancy-abundance patterns can predict each other very well in a variety of single and multiple species situations. The Nachman model has traditionally been used in agricultural entomology for estimating pest abundance. Its popularity stems from its computational simplicity and independence of its parameters from the assumptions of a specific distribution. The General model was as good as the Nachman model in predicting the occupancy of the

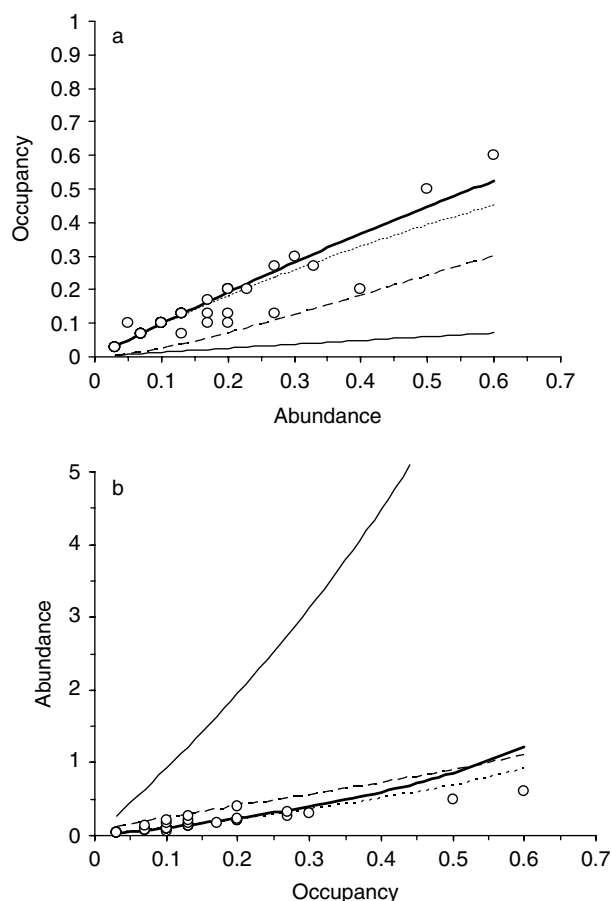


Fig. 5. Observed and predicted occupancy (proportion of plants infested) versus observed abundance (density per plant) (a) and observed abundance and abundance predicted from occupancy (b) of *Oothecca* in sesbania in southern Africa (o, observed; ---, General model;, Poisson model; —, negative binomial distribution (NBD) model; —, Nachman model).

three beetle species studied, and appears to have much wider potential application in economic entomology. Like the General model, Wilson & Room's (1983) model also incorporates Taylor's power law into the NBD, and it has been widely used in deriving binomial sampling plans. However, due to its computational complexity and distribution assumption (Kuno, 1986; Yaninek *et al.*, 1991), it has not been used in this study.

Counting individual insects is not only time consuming but it can also be extremely difficult to obtain an unbiased estimate with conventional sampling procedures, because insects such as *M. ochroptera* drop while *Exosoma* and *Oothecca* quickly fly away when disturbed. Large numbers of these beetles occur during the rainy season which often coincides with the period when sesbania plants in farmers' fields are most vulnerable to beetle damage (Sileshi *et al.*, 2000, 2003). Advance information about beetle populations is needed for decision-making in pest management. However, obtaining accurate density estimates using enumerative methods are largely impractical. The occupancy-abundance relationships established here can be used as guide to estimate beetle densities for decision-making. It is hoped that this will greatly

reduce sampling efforts in routine monitoring programmes, and save time and money without compromising accuracy. However, when using these models to predict abundance, a problem that has not been addressed here but must be kept in mind is that of imperfect detection of species (MacKenzie *et al.*, 2002). Lack of detection of a species may mean that the species is truly absent or is missed because of insufficient survey efforts (He & Gaston, 2003). Factors that influence detectability may vary spatially and temporally, and thus variations in observed counts cannot be attributed solely to variation in abundance (Royle *et al.*, 2005). Therefore, such factors need to be taken into account.

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