1 **Iwao's patchiness regression through the origin: biological importance and efficiency of**
2 **sampling applications**

3 Edward Kyle Waters · Michael J.Furlong · Kurt K. Benke · James Robin Grove · Andrew John
4 Hamilton

5 Edward Kyle Waters Melbourne School of Land and Environment, The University of
6 Melbourne, Parkville, Victoria 3010, Australia Tel.: +61-425-567-655 Fax: +61-2-8204-4422 E-
7 mail: edward.waters.nsw@gmail.com

8 Michael J. Furlong School of Biological Sciences, The University of Queensland, St Lucia,
9 Queensland 4072, Australia

10 Kurt K. Benke Department of Primary Industries, Parkville Centre,32 Lincoln Square North,
11 Carlton Victoria 3053, Australia

12 James R. Grove Melbourne School of Land and Environment, The University of Melbourne,
13 Parkville, Victoria 3010, Australia.

14 Andrew John Hamilton Melbourne School of Land and Environment, The University of
15 Melbourne, Parkville, Victoria 3010, Australia.

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Abstract: Iwao's mean crowding-mean density relation can be treated both as a linear function describing the biological characteristics of a species at a population level, or a regression model fitted to empirical data (Iwao's patchiness regression). In this latter form its parameters are commonly used to construct sampling plans for insect pests, which are characteristically patchily distributed or overdispersed. It is shown in this paper that modifying both the linear function and statistical model to force the intercept or lower functional limit through the origin results in more intuitive biological interpretation of parameters and better sampling economy. Firstly, forcing the function through the origin has the effect of ensuring that zero crowding occurs when zero individuals occupy a patch. Secondly, it ensures that negative values of the intercept, which do not yield an intuitive biological interpretation, will not arise. It is shown analytically that sequential sampling plans based on regression through the origin should be more efficient compared to plans based on conventional regression. For two overdispersed data sets, through-origin based plans collected a significantly lower sample size during validation than plans based on conventional regression, but the improvement in sampling efficiency was not large enough to be of practical benefit. No difference in sample size was observed when through-origin and conventional regression based plans were validated using underdispersed data. A field researcher wishing to adopt a through-origin form of Iwao's regression for the biological reasons outlined above can therefore be confident that their sampling strategies will not be affected by doing so.

Keywords Mathematical biology · Mean crowding · Sequential sampling.

Introduction

Iwao's (1968) regression of mean crowding (m^*) on mean density (m) has been one of the two major methods used for quantifying the variance-mean relation, the other being Taylor's Power Law (Taylor 1961). Kuno's (1969) and Green's (1970) sampling plans are based on Iwao's patchiness regression and Taylor's Power Law, respectively, and have been widely used in applied entomology. Their widespread use has generated much comparison of the two underlying models (Taylor 1984; Barker and Smith 1987; Fowler and Lynch 1987; Binns et al. 2000; Tokeshi 1995). The parameters of the debate have mostly converged on which model fits most data sets better, in general concluding that neither model is superior (Tokeshi 1995; Tonhasca et al. 1996; Lomic 2001), but only rarely acknowledging the quite different assumptions and approaches behind the two models (Ito and Kitching 1986). Taylor's Power Law was primarily adopted based on its fit to a wide range of field data (Taylor 1961, 1984; Taylor et al. 1978, 1979, 1980; Taylor and Woiwood 1980) but Iwao's patchiness regression, like Lloyd's mean crowding on which it was based, was devised as a model of biology in the first instance, with its fit to empirical data a secondary consideration (Lloyd 1967; Iwao 1968). Taylor intended that the parameters of his model would be unique to each species and constant over all ranges (Taylor 1961). Iwao never intended that the parameters of his model be constant for an individual species, but rather reflect biological processes affecting a population at a particular time, based on population and time specific field data (Iwao 1968). It is Iwao's emphasis on the biological foundation of parameter values that make Iwao's model, rather than Taylor's, the focus of this paper.

Iwao's (1968) model is:

$$m^* = a + bm \quad (1)$$

where b and a are the slope and intercept of the m^* - m line, with m being the mean density and m^* being Lloyd's mean crowding index (Lloyd 1967). The mean crowding index can also be expressed in terms of the variance V as:

$$m^* = m + \frac{V}{m} - 1 \quad (2)$$

Part of the reason that theoretically important insights can be made using this model is that whilst Iwao calls it a regression, he often treats it as a functional relationship between m^* and m , suggesting that in the presence of population level data (rather than sample data) the relationship can be analysed as a mathematical function. Indeed, in his development of the m^* index, Lloyd (1967) treats the population level index as a function of the arithmetic mean, and Kuno (1969) argues that it is necessary that the variance be expressed as an explicit function of the mean for sequential sampling to produce accurate estimates: this is why he chooses to base his sequential sampling method on m^* . Therefore in this paper, we prefer the term m^* - m relation rather than patchiness regression where we wish to stress the functional nature of the linear relationship.

It attests to the significance of Iwao's (1968) paper that further insights on application and theory can still be derived from it after more than 50 years. One aspect that requires further thought is the biological meaning of the intercept parameter (Ito and Kitching 1986). Negative intercepts are possible but make no biological sense (Walker et al. 1988; Silver 2008), and they may not be significantly different to zero (Jones and Parrella 1984). Positive intercepts that are not significantly different from zero are also not uncommon (Jones and Parrella 1984; Pitcairn et al. 1994), and unlike negative intercepts, do have an intuitive biological interpretation. The

authors hypothesised that as the intercept of Iwao's $m^* - m$ relation was often not significantly different from zero (Jones and Parrella 1984), then regression through the origin might be appropriately used, eliminating the issue of the interpretation of negative intercepts as a by-product. This paper explores whether fixing Iwao's $m^* - m$ relation to go through the origin is theoretically justifiable, statistically advantageous given the methods used to estimate its parameters, and reduces the sample size required when used to design sequential sampling plans with no loss of sampling precision. Both analytical methods and resampling methods based on field data are employed.

The biological basis of regression through the origin

It has been established that were Iwao's $m^* - m$ relation applied to a population of patchily distributed individuals whose spatial dispersion was perfectly described by the Poisson or negative binomial distributions with a common k , its intercept should be equal to zero, the intercept only taking on a value greater than zero when colonies of gregarious organisms crowd each other (Iwao 1968; Patil and Stiteler 1973; Ito and Kitching 1986; Kuno 1988). In practice, distinguishing what constitutes a colony from a collection of autonomous individuals that happen to occupy the same patch may not be straightforward, and interpreting the values of the intercept under the assumption that it relates to mean colony size can be difficult. In particular, the interpretation of negative values of the intercept presents difficulties under this hypothesis. One interpretation is that this represents a repulsive effect between individuals (Tsai et al. 2000), but this is not intuitively compatible with the definition of Iwao (1968) that the intercept gives the average number of individuals within another's ambit, a quantity which is necessarily positive. An additional problem is that the quantity as defined by Iwao must

necessarily differ depending on the size of ambit, which can be defined arbitrarily, and at the limit, may consist only of the area immediately occupied by an individual (Kuno 1988). All these problems of interpretation are done away with if the intercept is set to zero. Setting the intercept to zero also yields the biologically satisfactory conclusion of meaning that when there are zero individuals in a patch, the crowding exerted on them by each other is also zero, as opposed to being the average number of individuals they might encounter in another patch. Setting the intercept to equal zero also allows a more intuitive interpretation of the intercept parameter, allowing its explicit connection to the dispersion parameters of probability distributions to emerge more clearly. Iwao (1968) wrote that the slope parameter b is related to the dispersion parameter k of the negative binomial distribution by the formula:

$$b = 1 + \frac{1}{k} \quad (3)$$

When k approaches zero, indicating extreme over dispersion, m^* changes dramatically with mean density, and when k becomes large, indicating near-random distribution, m^* changes little with mean density (Southwood 1978). Thus it is clear that rewriting Eq. 1 as $m^* = b \times m$ will be adequate to describe the $V - m$ relationship for species with a range of spatial distributions.

Application of regression through the origin in sequential sampling: theoretical aspects

Despite sound mathematical and biological arguments for using a through-origin version of Iwao's $m^* - m$ relation, the effect of using regression through the origin on applications of the

model would need to be considered before such an approach could be advocated. The most common application of Iwao's m^* - m relation is the design of sequential sampling plans based on Kuno's method (Kuno 1969; Jones and Parrella 1984; Allsopp and Bull 1989; Pena and Baranowski 1990; Waters et al. 2009).

In Kuno's sampling plan, a site (say a field) is sampled to estimate the density of a target organism with a fixed level of precision (D), calculated by:

$$D = \frac{\frac{SD}{\sqrt{n}}}{\bar{x}} \quad (4)$$

where SD is the standard deviation in sample estimate of m ($\bar{x}$) and n is the number (n) of sampling units collected (Kuno 1969; Waters et al. 2009). Normally, $D = 0.3$ is used as a standard for the fixed level of precision (Barney and Legg 1988; Hutchison et al. 1988; Garat et al. 1999; Shah et al. 2000; Waters et al. 2009). The minimum sample size required to estimate density is given by the formula (Kuno 1969):

$$n_{min} = \frac{\left[\frac{(a+1)}{\bar{x}} + (b-1) \right]}{D^2} \quad (5)$$

As the sample size increases from n_{min} by one unit a cumulative tally (T_n) of the number of target organisms detected is compared to the value predicted by a stop line function (Kuno 1969):

$$T_n = \frac{(a+1)}{\left(D^2 - \left[\frac{(b-1)}{n_{min}} \right] \right)} \quad (6)$$

When the cumulative tally of target organisms collected is greater than the value at the stop line, sampling is terminated (Kuno 1969; Waters et al. 2009).

Mathematically, it would appear that setting the intercept to zero would result in a lower required sample size. The slope only affects the gradient of the T_n curve, so the sample size

required at the limit is entirely a function of desired precision and of the intercept, with lower intercepts requiring lower sample size at the limit (Kuno 1969). Theoretically therefore, plans based on negative intercepts should require even lower sample sizes than plans based on fixing the intercept at zero (see Fig. 1). However, the interpretation of negative intercepts is not biologically straightforward (Iwao 1968), as noted above, and negative intercepts are sufficiently rare not to be considered in Kuno's original paper (he only considered $a \geq 0$ and $b \geq 1$) (Kuno 1969). Whilst these results are interesting, it is not clear whether they would actually result in greater sampling efficiency when plans based on regression through the origin were implemented in the field. To confirm this, in this paper resampling methods were used to investigate the performance of sampling plans based on both conventional and through the origin regressions.

Comparison of through the origin and conventional regression based sampling plans – field data

Through the origin and standard regressions were fitted to three data sets using the R programming language (www.r-project.org). One data set described the numbers of arthropod pest larvae per plant in Brassica crops in the Democratic People's Republic of North Korea (DPRK), one the number of pest eggs in the same location, and another described the numbers of Cyclamen flowers (*Cyclamen* spp.) on plants in a Danish field trial. It has been suggested that model II regression be used for estimating the parameters of Iwao's $m^* - m$ relation (Waters et al. 2009). Model II regression is often recommended when the independent variable is subject to error, (Patil and Stiteler 1973; Sokal and Rohlf 1995) as with $\bar{x}$ in Iwao's Patchiness Regression (Waters et al. 2009). However, in this paper we used ordinary least squares

regression as recommended by Legendre (1998) since our data did not meet the bivariate normality assumption of model II regression.

The data from the DPRK was the same as used in Waters et al. (2009). These data originate from field studies conducted from 2003-2005 in cabbage crops (*Brassica oleracea* var. *capitata* cv. 6 – 21) in three mixed vegetable farms within a 70-km radius of Pyongyang. Field counts of Diamond Back Moth (*Plutella xylostella*) and *Pieris rapae* larvae, eggs and pupae were complied by haphazardly sampling 60 plants in each of 163 fields (Waters et al. 2009). In four additional fields, only 30 plants were sampled (Waters et al. 2009). Pest management regimes changed in each year of the study but are not relevant to this paper – for full details of the field studies see Furlong et al. (2008).

In Waters et al. (2009) Iwao's m^* - m relation was fitted to estimates of x^* and $\bar{x}$ for *P. rapae* larvae from 2003 and 2005 (92 data sets), and a sampling plan based on this regression validated using 2004 data (47 data sets). The parameters of Iwao's m^* - m relation were also estimated for *P. xylostella* larvae using the same data but a sampling plan based on the regression parameters was not validated. In this paper we validate one sampling plan for *P. xylostella* based on the conventional regression previously fitted, and also one based on the parameters of a regression through the origin. The through the origin regression was also fitted using the 2003 and 2005 data. Data from 2004 (47 fields) are used for validation of both plans. The DPRK data also contained egg counts per plant that were relatively reliable for *P. rapae*, as the eggs of this species are large and easy to sample in the field. We fitted Iwao's m^* - m relation both conventionally and through the origin to estimates of x^* and $\bar{x}$ for *P. rapae* egg data from 2003 and 2005 (92 data sets) and validated plans based on these regressions using 2004 data (47 data sets). Details of the methods used for validation follow the description of Cyclamen data used.

Labouriau (2011) contributed data giving the number of Cyclamen flowers per plant to the Australasian Data and Story Library (OzDASL, <http://www.statsci.org/data>). These data give the numbers of flowers for four varieties of Cyclamen subjected to combinations of six different temperature regimens and four different fertiliser regimens (96 combinations of variety, temperature regimen and fertiliser regimen represented overall). There were 20 plants in each combination tested, giving 1920 data points overall. The data were sorted in ascending order by variety, temperature regimen and fertiliser regimen using Microsoft Excel. Mean, variance and mean crowding were calculated for each of the first 40 combinations and used to estimate the parameters of conventional and through-origin regressions, and plans based on these parameters were validated using the remaining data from the remaining 56 combinations. Though sequential sampling plans are not normally used for estimating the mean number of flowers per plant, doing so would not differ mathematically from estimating the number of insects per plant. More importantly, the use of this data set adds rigour to this paper as the data are regularly distributed whereas the entomological data sets employed all conform to overdispersed distributions. Comparison of implementing conventional and through-origin based sampling plans on regularly distributed data allows easier generalisation about the performance of through-origin plans on data sets fitting different types of distributions.

Sampling plans were validated using code written in the C programming language. The algorithms employed were as described in Naranjo and Hutchison (1997) in their RVSP program but C was used to facilitate the use of a Unix-based computing environment and for computational efficiency – a typical resampling exercise took less than a second of computational time and outputted data in a spreadsheet formatted for instantaneous analysis using R. For each set of regression parameters, 500 resampling iterations were conducted on each data set. The minimum sample size was set as 10 for all resampling bouts. A uniform minimum sample size was preferred to ensure the fairest possible comparison between the

performance of plans based on conventional and through origin regressions. As noted above, plans based on through-origin regression will always demand a smaller sample size than those based on conventional regression when (5) is used to calculate minimum sample size. As mean sample size is a key aspect of evaluating sampling plan performance, with lower sample sizes being preferred, using a uniform minimum sample size ensured against unfairly preferencing through-origin plans at the outset. Resampling was with replacement. Two sample t tests were used to compare mean precision achieved and mean sample size collected during validation. R 2.15.2 for Windows (www.r-project.org) was used for statistical analysis. P values less than 0.05 were assumed to imply statistically significant differences between means.

Conventional regression lines fitted to DPRK data showed that both *P. xylostella* larvae and *P. rapae* eggs were overdispersed ($b > 1$ for all regressions, $a > 0$ for all conventional regressions). Conventional and through-origin regression lines for larvae and eggs and are shown in Figs. 2 and 3. On the other hand, Cyclamen flowers were more regularly distributed ($a < 0$ for conventional regression, $b < 1$ for regression through the origin). Conventional and through-origin regression lines for Cyclamen flowers are shown in Fig. 4. In cases the intercept of the conventional regression was significantly different from zero, and in all but one case (*P. xylostella*) the slopes of conventional and through origin regressions were significantly different. These results are summarised in Table 1. These results did not always correspond to significant differences in the performance of sampling plans based on regressions with significantly different parameters.

For each of the plans, the average sample size collected and precision achieved in resampling are shown in Table 1. Where data were overdispersed (both DPRK based plans), sampling plans based on through-origin regressions demanded significantly lower sample sizes, regardless of

whether the slopes of through-origin and conventional regressions were significantly different. Regardless of significant differences in sample size collected, precision did not differ between plans based on through-origin and conventional regressions. For plans based on regularly distributed data with a negative intercept in conventional regression (Cyclamen data), no advantage was gained by using through-origin regression as neither mean sample size collected or precision achieved improved.

Discussion

There are powerful mathematical and biological reasons against having a non-zero intercept in Iwao's $m^* - m$ relation. Though often called a regression, it is really a functional relationship describing the changes in the mean number of individuals in an area with increasing aggregation, and it is not possible to have a negative number of individuals in an area. It is also unclear how there can be a positive mean crowding value (positive intercept) when the mean density of individuals is zero. These arguments are of diminished value if a non-zero intercept provides advantages to application of the model in the real world, where it is primarily used in designing sampling plans.

The validation of sampling plans using two data sets giving counts of insect larvae and eggs showed that on the contrary, setting the intercept to zero is likely to be beneficial to the application of Iwao's $m^* - m$ relation. For these overdispersed data, using sampling plans based on regression through the origin resulted in the collection of slightly fewer samples during validation and no loss of sampling precision. These results were especially encouraging

because the intercepts of conventional regressions based on the same data were significantly greater than zero, supporting analytical conclusions drawn from inspecting the stop-lines (see Fig. 1) that zero intercepts would result in an improvement in sampling efficiency compared to non-zero intercepts. The improvements in sampling efficiency (sample size required reduced by two or three plants) were not substantial, however, and would be unlikely to be a critical factor in deciding to employ plans based on regression through the origin. Regression through the origin is therefore to be preferred for biological reasons, and the fact that there is no difference of practical significance between plans based on conventional and through-origin regressions is an additional positive.

Just as there were no negative consequences of practical significance to employing plans based on regression through the origin for overdispersed data, there were also no negative consequences to employing through-origin based plans for regularly distributed data. When plans based on regression through the origin and conventional regressions were designed and validated using underdispersed data from a floriculture field trial, there was no benefit to using regression through the origin but no drawbacks either, with sampling intensity and precision not differing with parameterisation. This suggests that using regression through the origin might at worst make no difference to the performance of sampling plans based on Iwao's m^* - m relation, and at best be beneficial. Future studies comparing the effect of regression through the origin and conventional regression on the performance of sampling plans should test this assumption using a wider variety of data sets, but the preliminary findings contained in this paper are intriguing.

Conclusion

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301 There are a number of reasons to prefer using Iwao's $m^* - m$ relation forced through the origin
302 to describe patchily distributed organisms, especially when sampling applications based on the
303 regression parameters are planned. Firstly, setting the intercept to the origin has the
304 biologically satisfying effect of ensuring that zero crowding occurs when zero individuals
305 occupy a patch. Secondly, it ensures that negative values of the intercept will not arise, with
306 the difficulties in interpretation described above. Based on analysis of the formulae used to
307 calculate the stop line of Kuno's sampling plan, regression through the origin should lead to
308 more efficient sampling plans in terms of sampling intensity when compared to the same data
309 fitted to a regression with a positive intercept. In this paper this analytical conclusion was
310 tested empirically. A lower sample size was required by sampling plans based on regression
311 through the origin when the intercept of the conventional regression was significantly
312 different from zero, though this sample size did not differ by enough to be of practical
313 importance. No benefit was found to using regression through the origin for regularly
314 distributed data with a negative intercept in conventional regression. However, there was no
315 loss of sampling precision or increase in sample size from using regression through the origin in
316 this situation. Not only, therefore, does an intercept at the origin of Iwao's $m^* - m$ relation
317 more accurately reflect the biology of organisms for whom sampling plans are required, but
318 sampling plans based on regression through the origin can perform better than those based on
319 conventional regression, supporting the conclusions arrived through analytical means. Even if
320 the degree of improvements in sampling efficiency were not large enough to induce
321 preference for regression through the origin on their own, they provide reassurance to the
322 field researcher that adoption of the strategy for biological reasons will have no adverse
323 effects on sampling performance.

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Table 1 Mean sample size collected (n) and precision achieved (D) in resampling using the parameters for standard and through-origin regressions. For each of the three species studied, we highlight where parameter estimates or results presented on consecutive lines are significantly different.

Species	Model	Intercept (95% CI) a	Slope (95% CI) b	Mean (SD) n	Mean (SD) D
<i>P. xylostella</i>	Standard	0.309 (0.138,	1.323 (1.244,	12.215	0.011
		0.479) ^a	1.402)	(1.987) ^b	(0.011)
	Through- origin	0.000 ^a	1.392 (1.318,	11.756	0.011
			1.465)	(1.323) ^b	(0.011)
<i>P. rapae</i>	Standard	0.598 (0.361,	1.510 (1.415,	21.824	0.032
		0.834) ^c	1.603) ^d	(4.072) ^e	(0.012)
	Through- origin	0.000 ^c	1.648 (1.563,	18.058	0.031
			1.734) ^d	(2.663) ^e	(0.011)
<i>Cyclamen</i>	Standard	-1.693 (-	1.150 (1.083,	11.000	0.002
		2.245,-1.140) ^f	1.217) ^g	(0.000)	(0.001)
	Through- origin	0.000 ^f	0.946 (0.938,	11.000	0.002
			0.954) ^g	(0.000)	(0.001)

^{a,b,c,d,e,f,g} Pairs of parameter estimates or means which differ at 0.05 level

423

424 **Figure 1** As the intercept a gets smaller, the total sample size required (n) and the cumulative
425 number of organisms collected (T_n) declines. For each intercept value a , two lines are
426 presented; the upper has slope $b = 1.1$ and the lower slope $b = 2.0$. $D = 0.3$.

427

428

429 **Figure 2** Comparison of conventional (solid line) and through-origin (dashed line) regression
430 lines for *P. xylostella* larvae. Regression parameters are ($a = 0.309$, $b = 1.323$) and ($a = 0.000$, b
431 $= 1.392$).

432

433 **Figure 3** Comparison of conventional (solid line) and through-origin (dashed line) regression
434 lines for *P. rapae* eggs. Regression parameters are ($a = 0.598$, $b = 1.510$) and through-origin (a
435 $= 0.000$, $b = 1.648$).

436

437 **Figure 4** Comparison of conventional (solid line) and through-origin (dashed line) regression
438 lines for *Cyclamen* flowers. Regression parameters are ($a = -1.693$, $b = 1.150$) and through-
439 origin ($a = 0.000$, $b = 0.946$)

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Author/s:

Waters, EK;Furlong, MJ;Benke, KK;Grove, JR;Hamilton, AJ

Title:

Iwao's patchiness regression through the origin: biological importance and efficiency of sampling applications

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