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Title:

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Date:

2014-01-01

Citation:

Waters, E. K., Furlong, M. J., Benke, K. K., Grove, J. R. & Hamilton, A. J. (2014). Iwao's patchiness regression through the origin: Biological importance and efficiency of sampling applications. *Population Ecology*, 56 (2), pp.393-399. <https://doi.org/10.1007/s10144-013-0417-y>.

Persistent Link:

<https://hdl.handle.net/11343/282947>

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

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17 Number of text pages: 15

18 Number of figures: 4

19 Number of tables: 1

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

40 **Keywords** Mathematical biology · Mean crowding · Sequential sampling.

41

42 **Introduction**

43

44 Iwao's (1968) regression of mean crowding (m^*) on mean density (m) has been one of the two
45 major methods used for quantifying the variance-mean relation, the other being Taylor's
46 Power Law (Taylor 1961). Kuno's (1969) and Green's (1970) sampling plans are based on
47 Iwao's patchiness regression and Taylor's Power Law, respectively, and have been widely used
48 in applied entomology. Their widespread use has generated much comparison of the two
49 underlying models (Taylor 1984; Barker and Smith 1987; Fowler and Lynch 1987; Binns et al.
50 2000; Tokeshi 1995). The parameters of the debate have mostly converged on which model
51 fits most data sets better, in general concluding that neither model is superior (Tokeshi 1995;
52 Tonhasca et al. 1996; Lomic 2001), but only rarely acknowledging the quite different
53 assumptions and approaches behind the two models (Ito and Kitching 1986). Taylor's Power
54 Law was primarily adopted based on its fit to a wide range of field data (Taylor 1961, 1984;
55 Taylor et al. 1978, 1979, 1980; Taylor and Woiwood 1980) but Iwao's patchiness regression,
56 like Lloyd's mean crowding on which it was based, was devised as a model of biology in the
57 first instance, with its fit to empirical data a secondary consideration (Lloyd 1967; Iwao 1968).
58 Taylor intended that the parameters of his model would be unique to each species and
59 constant over all ranges (Taylor 1961). Iwao never intended that the parameters of his model
60 be constant for an individual species, but rather reflect biological processes affecting a
61 population at a particular time, based on population and time specific field data (Iwao 1968). It
62 is Iwao's emphasis on the biological foundation of parameter values that make Iwao's model,
63 rather than Taylor's, the focus of this paper.

64

65 Iwao's (1968) model is:

66
$$m^* = a + bm \tag{1}$$

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

70
$$m^* = m + \frac{V}{m} - 1 \tag{2}$$

71

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

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

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

97

98 **The biological basis of regression through the origin**

99

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

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

123

$$124 \quad b = 1 + \frac{1}{k} \quad (3)$$

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

130

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

132

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

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

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

$$141 \quad D = \frac{\frac{SD}{\sqrt{n}}}{\bar{x}} \quad (4)$$

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

$$147 \quad n_{min} = \frac{\left[\frac{(a+1)}{\bar{x}} + (b-1) \right]}{D^2} \quad (5)$$

148 As the sample size increases from n_{min} by one unit a cumulative tally (T_n) of the number of
 149 target organisms detected is compared to the value predicted by a stop line function (Kuno
 150 1969):

$$151 \quad T_n = \frac{(a+1)}{\left(D^2 - \left[\frac{(b-1)}{n_{min}} \right] \right)} \quad (6)$$

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

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

156 required at the limit is entirely a function of desired precision and of the intercept, with lower
157 intercepts requiring lower sample size at the limit (Kuno 1969). Theoretically therefore, plans
158 based on negative intercepts should require even lower sample sizes than plans based on
159 fixing the intercept at zero (see Fig. 1). However, the interpretation of negative intercepts is
160 not biologically straightforward (Iwao 1968), as noted above, and negative intercepts are
161 sufficiently rare not to be considered in Kuno's original paper (he only considered $a \geq 0$ and
162 $b \geq 1$) (Kuno 1969). Whilst these results are interesting, it is not clear whether they would
163 actually result in greater sampling efficiency when plans based on regression through the
164 origin were implemented in the field. To confirm this, in this paper resampling methods were
165 used to investigate the performance of sampling plans based on both conventional and
166 through the origin regressions.

167

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

170

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

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

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

190 In Waters et al. (2009) Iwao's $m^* - m$ relation was fitted to estimates of x^* and \bar{x} for *P. rapae*
191 larvae from 2003 and 2005 (92 data sets), and a sampling plan based on this regression
192 validated using 2004 data (47 data sets). The parameters of Iwao's $m^* - m$ relation were also
193 estimated for *P. xylostella* larvae using the same data but a sampling plan based on the
194 regression parameters was not validated. In this paper we validate one sampling plan for *P.*
195 *xylostella* based on the conventional regression previously fitted, and also one based on the
196 parameters of a regression through the origin. The through the origin regression was also
197 fitted using the 2003 and 2005 data. Data from 2004 (47 fields) are used for validation of both
198 plans. The DPRK data also contained egg counts per plant that were relatively reliable for *P.*
199 *rapae*, as the eggs of this species are large and easy to sample in the field. We fitted Iwao's m^*
200 $- m$ relation both conventionally and through the origin to estimates of x^* and \bar{x} for *P. rapae*
201 egg data from 2003 and 2005 (92 data sets) and validated plans based on these regressions
202 using 2004 data (47 data sets). Details of the methods used for validation follow the
203 description of Cyclamen data used.

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

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

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

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

249

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

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

259

260 **Discussion**

261

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

270

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

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

285

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

298

299 **Conclusion**

300

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.

324

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414 **Table 1** Mean sample size collected (n) and precision achieved (D) in resampling using the
 415 parameters for standard and through-origin regressions. For each of the three species studied,
 416 we highlight where parameter estimates or results presented on consecutive lines are
 417 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, 0.479) ^a	1.323 (1.244, 1.402)	12.215 (1.987) ^b	0.011 (0.011)
	Through- origin	0.000 ^a	1.392 (1.318, 1.465)	11.756 (1.323) ^b	0.011 (0.011)
<i>P. rapae</i>	Standard	0.598 (0.361, 0.834) ^c	1.510 (1.415, 1.603) ^d	21.824 (4.072) ^e	0.032 (0.012)
	Through- origin	0.000 ^c	1.648 (1.563, 1.734) ^d	18.058 (2.663) ^e	0.031 (0.011)
<i>Cyclamen</i>	Standard	-1.693 (- 2.245,-1.140) ^f	1.150 (1.083, 1.217) ^g	11.000 (0.000)	0.002 (0.001)
	Through- origin	0.000 ^f	0.946 (0.938, 0.954) ^g	11.000 (0.000)	0.002 (0.001)

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

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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 $b = 2.0$. $D = 0.3$.

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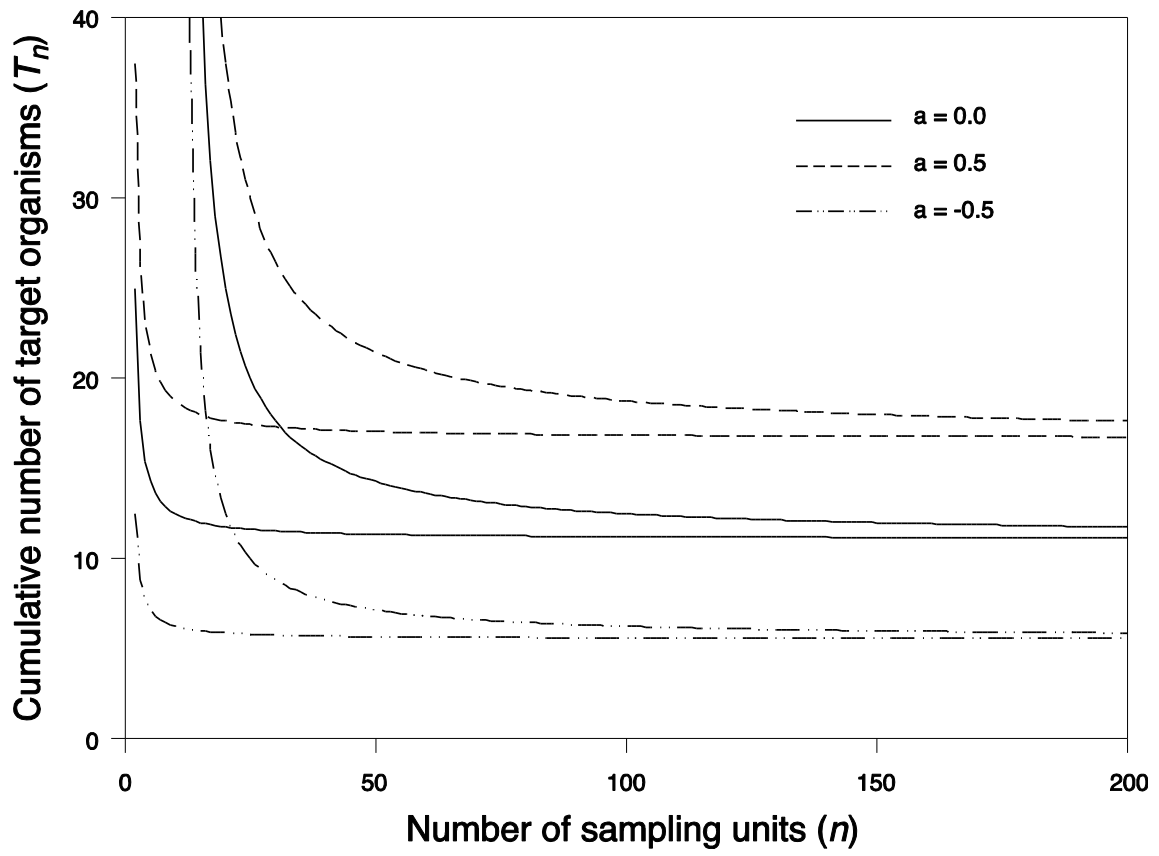
429 **Figure 2** Comparison of conventional (solid line) and through-origin (dashed line) regression
430 lines for *P. xylostella* larvae. Regression parameters are ($a = 0.309$, $b = 1.323$) and ($a = 0.000$, b
431 $= 1.392$).

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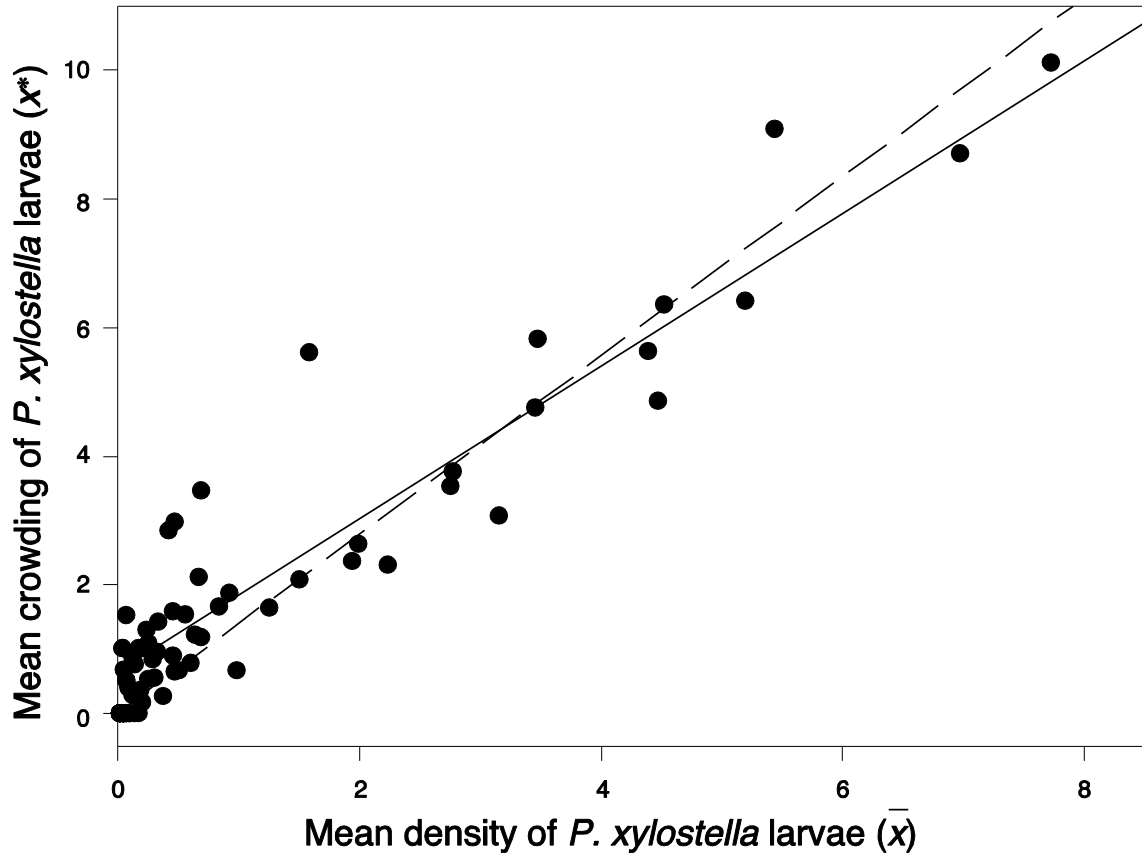
433 **Figure 3** Comparison of conventional (solid line) and through-origin (dashed line) regression
434 lines for *P. rapae* eggs. Regression parameters are ($a = 0.598$, $b = 1.510$) and through-origin (a
435 $= 0.000$, $b = 1.648$).

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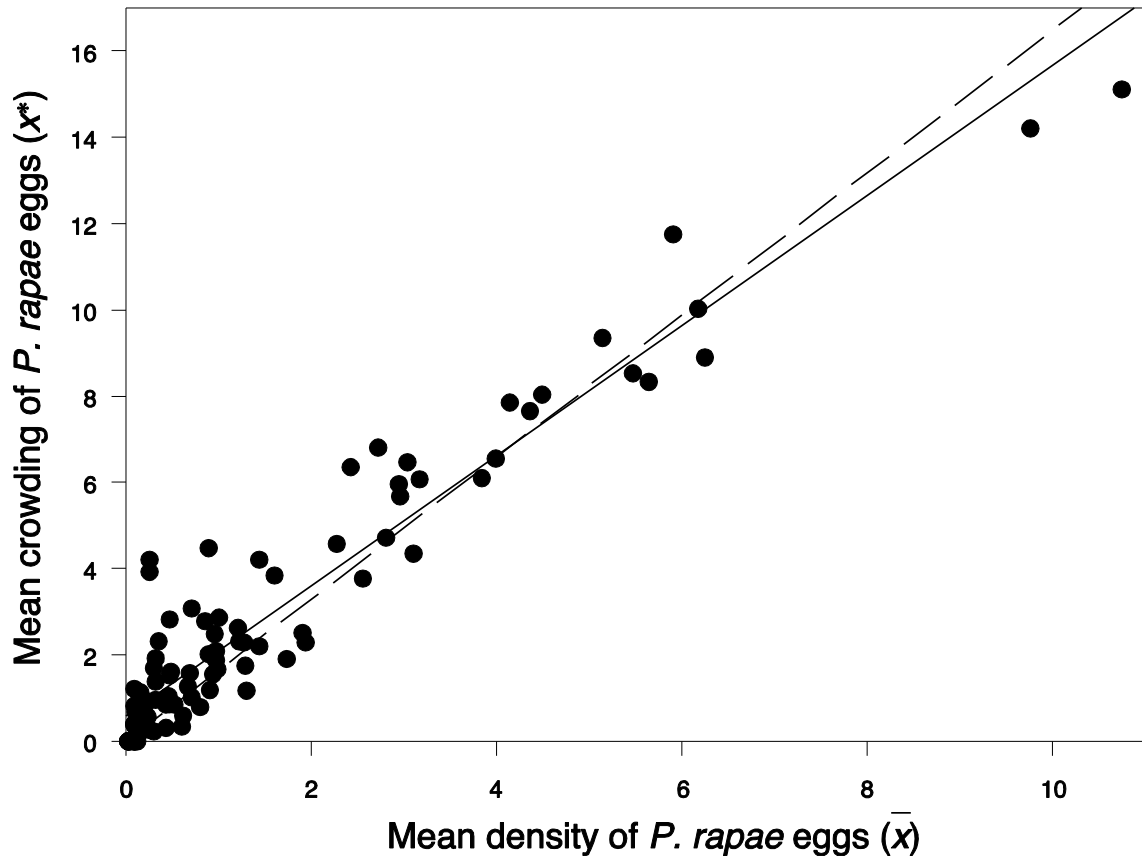
437 **Figure 4** Comparison of conventional (solid line) and through-origin (dashed line) regression
438 lines for *Cyclamen* flowers. Regression parameters are ($a = -1.693$, $b = 1.150$) and through-
439 origin ($a = 0.000$, $b = 0.946$)



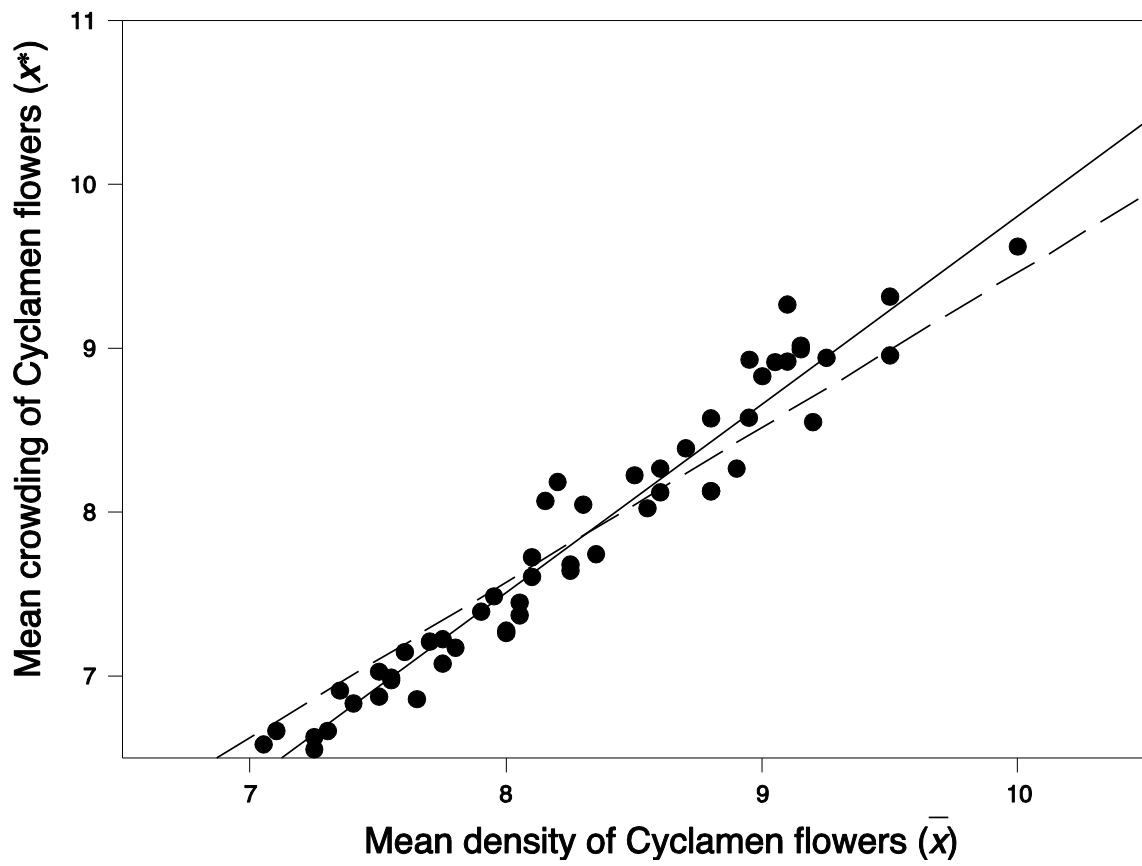
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