OLM 4.1. Age or size classification for plants

It has been stressed in Ch4Struct that not even a thorough knowledge of the biology of a species makes it always apparent how to define the relevant *i*-states. We will take a closer look at this problem here, recalling details of the example already mentioned in the book of two semelparous plant species (*Dipsacus sylvestris* and *Verbascum thapsus)* – both classified as biennial but often showing a longer life span in their natural habitats. Individual plants both of these species – have been shown to be adequately qualified on the basis of rosette size in order to predict their fate and the growth of their populations (TBE, p. 50).

The only general guideline for the proper choice of *i*-states is that the state groups should be sufficiently homogeneous, in terms of the expected distributions of their dynamical behaviour (rates of survival, reproduction and *i*-state transitions). For choosing the most appropriate *i*-state variable we have to analyse the strength of the relation between the potential *i*-state variables and the response variables. The possible *i*-state variables may be either discrete or continuous. We may choose to transform the latter to categorical variables, but this plays no role in assessing their importance. The response variable may be a vital rate, or individual fate between two censuses (itself determined by a number of vital rates). If the fecundity of the species is high, then it can be a count or continuous variable, if it is small, then the fecundity variable is conveniently categorical, and it is binary for species in which the number of offspring is fixed. Survival between two censuses is a binary variable (survives/dies).

Independently of the actual types of the variables it has to be decided in all cases whether the state variables considered do interfere with each other's effect; i.e., if there is interaction between them. A frequently asked question for plants concerns whether both their size and age affect their vital rates and if yes, whether they act independently or in interaction. If – like in the *Lavandula* example of Figure 4.1.1 – age would have a significant influence on the effect of size (or vice versa), then these two variables would be in interaction (statistically) and we should use combined size/age *i*-states. Without such interactions we have to test for the partial effects of the two *i*-state variables on the response variable. If, for example, size in itself explains a much larger proportion of the variation of the response variable than age does, then it may be sufficient to structure the population by size alone.

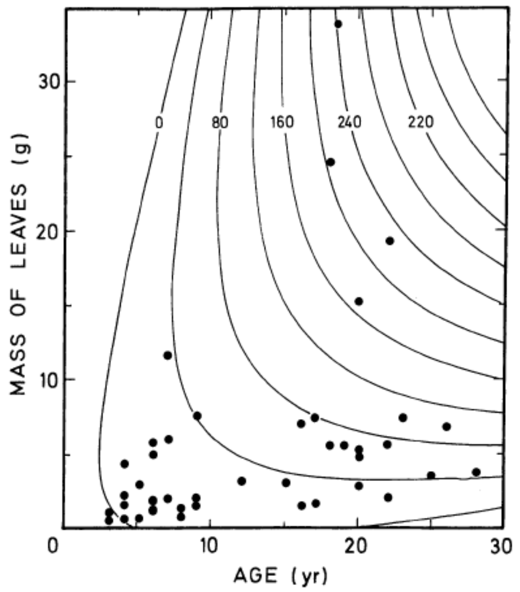

Figure 4.1.1 The number of inflorescences per plant of the long-lived individuals of *Lavandula angustifolia* (lavender) depends on both the size and the age of the plants.
Contour lines indicate iso-numbers of inflorescences fitted to the actual data; the dots are the observed age/size combinations. The model including the interaction of age and size explains 92.5% of the variation in the number of inflorescences (Herrera 1991).

Generalized linear models (GLM) are suitable for treating any particular case in a unified framework, independently from the actual type of *i*-state variable scale, by choosing a reference distribution according to the scale type of the response variable (binomial for binary, multinomial for categorical, and Poisson or negative binomial for count response variables). Ecologists interested in using the GLM method are advised to read the textbook of Fox, Negrete-Yankelevich and Sosa (2015). In case the data are non-Gaussian distributed the explained variability can be calculated from the model likelihoods (Ch2.7, p.27; OLM 2.3) using McFadden's pseudo R^2 values. If both the *i*-state and the response variables are categorical, then a log-linear contingency table analysis (the one used in the next example) would be an appropriate method for making the decision (Caswell 1988, Caswell 2001).

Two semelparous (reproducing once in a lifetime) plant species, the teasel (*Dipsacus sylvestris;* identical with *Dipsacus fullonum*) and the common mullein (*Verbascum thapsus*) which are biennial in gardens but may live as long as for 5 years otherwise, develop large, flat vegetative rosettes. The studies of Werner (1975) and Gross (1981) present data on how the future fate of the individual depends on the size and the age of its rosette. The response variable was the fate of the plant individual, which could take 3 possible values: death, survival in vegetative state, and survival and flowering. No significant interaction between the effects of age and size was detected in either species (Table 4.1.1).

Table 4.1.1 The effect of size and age on the fate of two "biennial" plant species (data from Werner (1975) and Gross (1981)).
The study has been based on log-linear contingency table analysis; the variation explained has been measured by Goodman-Kruskal τ (Caswell 1988, Caswell 2001).

	Dipsacus sylvestris				***Verbascum thapsus***			
	G^2	**d.f.**	**p**	**Explained variation(%)**	**G^2**	**d.f.**	**p**	**Explained variation (%)**
marginal effect of size	**1198.15**	**10**	**<0.001**	**39.0**	**628.7**	**10**	**<0.001**	**48.2**
marginal effect of age	**534.96**	**6**	**<0.001**	**13.9**	**19.01**	**2**	**<0.001**	**1.3**
parcial effect of size	**678.67**	**10**	**<0.001**	**29.8**	**612.07**	**10**	**<0.001**	**48.2**
parcial effect of age	**16.48**	**6**	**0.01**	**1.0**	2.38	2	0.31	1.4
size x age interaction	38.56	30	0.14	-	17.72	10	0.09	-

The fates of individuals were significantly affected by both age and size (marginal effects) in both species. Older individuals tend to be larger; therefore, the partial effects of these variables, i.e., the component of the age effect that is not explained by size, and the component of the size effect that is not explained by age, have to be analysed as well. The partial effect of age can be tested by checking how much the fit of the statistical model already considering the effect of size is improved by including the effect of age as well. For *Verbascum thapsus* the partial effect of age is insignificant, meaning that knowing the size of the individual the additional information regarding its age does not substantially improve the fit of the data to the model. The partial effect of size is significant, however; therefore, it is reasonable to choose size for the *i*-state of this species. For *Dipsacus sylvestris* the partial effects of both age and size are significant, but once size has been considered the addition of the age effect increases the variation explained only by 1%. Having considered the age, the addition of size effect explains an extra 30% of variation, however. That is, size is sufficient to use as the relevant *i*-state variable of this species as well. If the variation explained by the partial effects would have been high for both variables, then we should have used the combined *i*-state in spite of the fact that their effects are independent of each other. After the publication of these two pioneering studies it has been shown that for plant species classified as biennial it is generally true that they reproduce only after they have reached a certain minimum size (Kachi 2012), and the time required for this depends on the circumstances.

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