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Discussion comments on 'Evaluation of some random effects methodology applicable to bird ringing data' by Burnham & White

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This paper nicely demonstrates how an intermediate or combination approach to a problem offers benefits greater than those provided by more extreme approaches. In one instance, survival rates can be postulated, at the simplest extreme, to be identical for all groups (or years); this is the *no effects* model. At the other, most complex and highly parameterized, extreme, survival rates can be distinct for each group; this is the *fixed effects* model. Burnham & White show the advantages of an intermediate model, the *random effects* model, in which survival rates are assumed to vary randomly about some average value.

Analogously, estimates of means of different groups can be based on the grand mean (the simplest approach) or the means of observations in each group (the most complex approach). As Burnham & White as well as others have shown, however, a weighted average of the grand mean and a group mean often performs better as an estimator for that group. These are termed shrinkage estimators. Closely tied to shrinkage estimation is the question of whether or not to pool data from different groups.

It is intriguing to draw parallels to other issues, many of which were topics of the EURING 2000 conference (Table 1). For example, the use of covariates in statistical analysis can range from none, at the simplest extreme, to covariates specific to individuals, at the most complex. The use of group-specific covariates is intermediate. Likewise, parsimony reflects an intermediate state between the use of too few explanatory variables in an analysis and the use of too many. In addition, parsimony dictates an adequately fitting model, as opposed to a poorly fitting model, which might arise from the use of too few explanatory variables, or a perfectly fitting model, which might result from using too many. A parsimonious

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TABLE 1. Many issues can be viewed along a continuum, from simplest to most complex. Often intermediate approaches confer advantages offered by neither extreme.

Issue	Simplest	Intermediate	Most complex
Survival rate for groups (S_i)	$S_i = S$ (no effects)	$S_i = \mu + e_i$ (random effects)	S_i arbitrary (fixed effects)
Estimate of mean for group i	$\theta_i = \bar{X}$ (grand mean)	$\theta_i = w\bar{X}_i + (1 - w)\bar{X}$ (shrinkage estimator)	$\theta_i = \bar{X}_i$ (individual means)
Pooling of data among groups	total pooling	partial pooling	no pooling
Resolution of covariates	no covariates	group-level	individual-level
Number of explanatory variables in analysis	few	parsimonious	many
Fit of model to data	poor	adequate	perfect
Criterion minimized	variance	MSE or AIC	bias
Degree of abstraction	mathematical abstration		biological realism
Uniqueness of individuals	all are identical	some shared traits (statistical distribution)	each is unique
Understandability of system	much		little
Scientific perspective	mathematical		descriptive biology

model might be produced by minimizing a composite criterion such as mean squared error or Akaike's Information Criterion. In contrast, emphasis solely on reducing variance may generate too simple a model, whereas emphasis primarily on reducing bias might yield too complex a model.

The degree of abstraction produces a continuum between mathematical abstraction and biological realism. At the former extreme, all individuals can be considered identical; at the latter extreme, each individual can be viewed as unique. Often most useful is an intermediate position in which individuals share some traits—such as mass or survivorship—which might be considered as drawn from a statistical distribution. Assuming all individuals are identical implies that much can be understood from knowledge of even a single individual. Assuming each individual is unique implies that few generalizations can be made (Nichols, this issue). Clearly neither extreme provides the most useful approach to biological science.

Finally, a continuum can be conceived between mathematicians, whose abstractions invoke the loss of individual identities, and descriptive biologists, who may be intimately familiar with many animals and who know the unique traits of each. While scientists at either extreme make useful contributions, greater progress results from a consolidation of the two perspectives, a synergism reflected in the Burnham & White article and in others presented at this meeting.

REFERENCES

NICHOLS, J. D. (2002) Discussion comments 'Occam's shadow: levels of analysis in evolutionary ecology—where to next?' by Cooch, Cam, and Link, *Journal of Applied Statistics*, this issue.