Within-population heterogeneity in survival propensities is very widespread.

Causes

Genetic polymorphism, plasticity, social, dens-dep, maternal provisioning, social hierarchy, persistent envir heterogeneity

Studies of survival face an inherent difficulty: distinguishing between variation in survival probability, and stochastic variation. After all, if individual A dies at time *t* while individual B dies at *t+2*, do they differ in survival probability, or was on luckier than the other? The answer is that, with this data, we cannot tell. However, there are several approaches to identifying survival heterogeneity”

* Association of an identifiable phenotypic trait or state with survival. This is how studies of age-, size-, and stage-structured demography work (Caswell; Ellner & Rees). There are also well-established cases among both bacteria and fungi (CITES), in which certain molecular or developmental switches cause phenotypic changes that alter survival probabilities. FOR EXAMPLE,
* Comparison of groups (like families or stands) for survival.
* For individuals, one can compare the fit of a model allowing for survival heterogeneity at the individual level with that of a model that treats all individuals as identical.

Of course, heterogeneity may occur at multiple levels. There is no reason why (say) genetic or maternal effects may not co-occur with individual phenotypic variation. The causes of these effects could even interact with one another. But statistically it could be quite challenging to study hypotheses about heterogeneity at multiple levels, and the sample sizes necessary might be prohibitive.

Showing that heterogeneity occurs at one level does not preclude heterogeneity at others.

There is a vast literature on survival heterogeneity within populations. Two broad statistical (and modeling) approaches are used:

* Heterogeneity studied as a function of some covariate. Almost all studies use age, size, developmental stage, or a combination of these, to study survival. There are, of course, other factors – whether intrinsic to the organisms (like genotype) or extrinsic (like sun vs. shade) used in some studies.
* Heterogeneity treated as a random term. This may be a lumping-together of what is sometimes thought of as “noise,” or it may be a thoughtful model of variation. As such, this is analogous with approaches like GLMM, where one can simply attempt to “account for” variation among, say, plots, because blah blah. Or one might be estimating, say, variance among families.

Statistical approaches

K-M, AFT, Cox. A couple of sentences on each, giving refs.

Of course, logistic reg is also useful in many settings. But for assessing het, it’s frequently not as useful b/c it’s just asking what the chance of (those in a group) have of surviving. Can use all the hierarchical groupings of GLMM, but can’t think about indivs themselves.

Frailty. A random term, which can be done at different levels (but presently only at one in a model). Key frailty approaches: indiv, shared frailty

Vitality

MRR

Since variation among ages, sizes, and developmental stages is well accepted – in fact, the overwhelming majority of demographic studies includes these. So we don’t need examples here.

* Cam’s group
* Florida Scrub Jays
* Bighorn sheep?
* Drosophila – Service,
* Saino et al – Barn swallows
* Reid Choughs
* Carol Vleck
* Vindenes?

But what about other kinds of het? Variation among indivs, families, social groups, other?

## Animals

, mostly vertebrates

## Plants

John L. Harper, often regarded as the father of plant demography, was reputed to have remarked “It’s almost as if every plant has a Christian name.” This observation followed, of course, from the detailed studies he and his students made of the demographic performance of plants in Welsh pastures.

A shortcoming of the Harper school’s approach was that, the more heterogeneity they found, the more they pursued. Important as the Harperians were, their influence faded somewhat as the field turned to methods like matrix models. This amounted to bending the stick (or the pendulum, or whatever) in the other direction: other than age, stage, or size, ecologists ignored, or even denied, that there was more demographic heterogeneity in populations.

Almost all of the enormous number of studies on plant survival use the standard covariates (some combination of size, age, and stage). Not uncommonly many also use a spatial variable like plot, to account for the observed variation among locations.

## Human studies

Demogr

Clinical