

Evolutionary biology and life histories

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The demographic processes that drive the spread of populations through environments and in turn determine the abundance of organisms are the same demographic processes that drive the spread of genes through populations and in turn determine gene frequencies and fitness. Conceptually, marked similarities exist in the dynamic processes underlying population ecology and those underlying evolutionary biology. Central to an understanding of both disciplines is life history and its component demographic rates, such as survival, fecundity, and age of first breeding, and biologists from both fields have a vested interest in good analytical machinery for the estimation and analysis of these demographic rates.

In the EURING conferences, we have been striving since the mid 1980s to promote a quantitative understanding of demographic rates through interdisciplinary collaboration between ecologists and statisticians. From the ecological side, the principal impetus has come from population biology, and in particular from wildlife biology, but the importance of good quantitative insights into demographic processes has long been recognized by a number of evolutionary biologists (e.g., Nichols & Kendall, 1995; Clobert, 1995; Cooch et al., 2002). In organizing this session, we have aimed to create a forum for those committed to gaining the best possible understanding of evolutionary processes through the application of modern quantitative methods for the collection and interpretation of data on marked animal populations. Here we present a short overview of the material presented in the session on evolutionary biology and life histories.

In a plenary talk, Brown & Brown (2004) explored how mark–recapture methods have allowed a better understanding of the evolution of group–living and alternative reproductive tactics in colonial cliff swallows (*Petrochelidon pyrrhonota*). By estimating the number of transient birds passing through colonies of different sizes, they showed that the number of ectoparasites at a colony site depends in part on how many transient swallows visit and introduce bugs from outside the group. Brown & Brown (2004) found that annual survival was related to the likelihood of a bird engaging in extra–pair copulation or intraspecific brood parasitism and could thus infer the relative costs and benefits of these reproductive tactics. These authors also showed that first–year survival patterns can explain the observed clutch–size distribution, in which clutches of intermediate size tend to be the most productive in most years even though larger clutches always fledge more offspring. The importance of using mark–recapture for questions in behavioral ecology was emphasized by Brown & Brown's (2004) study.

The likelihood that a sexually mature individual chooses to breed in a given year was explored by Reed et al. (2004) in a study of greater snow geese (*Chen caerulescens atlantica*). By combining information from mark–recapture, telemetry, and nest surveys, these authors found that adult snow geese were more likely to breed in years with low snow cover and that breeding propensity was positively related to nest density in a given year. Reed et al.'s (2004) results illustrate surprisingly high variation in reproductive effort among geese between years and emphasize the importance of environmental conditions (in this case, the timing of spring snow melt) in determining reproductive success of snow geese and other arctic–nesting birds.

The trade–off between survival and reproduction, and to what degree this trade–off reflects a cost of reproduction, was addressed by Tavecchia et al. (2005) for Soay sheep (*Ovis aries*) and Rivalan et al. (pers. comm.) for leatherback sea turtles (*Dermochelys coriacea*). In sheep, the cost of reproduction was a quadratic function of a mother's age, being greatest for the youngest and oldest females, but this cost applied only during

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severe environmental conditions (cold and wet winters) that coincided with high population density (Tavecchia et al., 2005). The significant interaction between age and time may have been responsible for maintaining differences among cohorts in demographic parameters such as survival (Tavecchia et al., 2005). In turtles, Rivalan et al. (pers. comm.) found evidence of a typical cost of reproduction in which the number of reproductive seasons in an individual's lifetime was inversely related to the extent of reproductive investment in a given season. By statistically accounting for loss of tags in these turtles, which can be substantial and thus may potentially bias state–transition probabilities, the authors discovered that fitness was roughly equivalent for all females, regardless of how often they attempted to breed. The studies by Tavecchia et al. (2005) and Rivalan et al. (pers. comm.) illustrate the benefits of using multi–state models in accounting for recapture/re–sighting probabilities.

The pattern of senescence in wild populations was a focus of the work by Catchpole et al. (2004) and Gaillard et al. (2004). In the well–studied red deer (*Cervus elaphus*) of Rum, senility was suggested by a survival probability that declined with age among the oldest age classes in both males and females, although there was little evidence for age–dependent survival among the younger age classes (Catchpole et al., 2004). As in many species, some animals dispersed from the study area, and notably Catchpole et al. (2004) accounted for dispersal in their estimates of age–dependent survival. In a comparative study of roe deer (*Capreolus capreolus*) and bighorn sheep (*Ovis canadensis*), Gaillard et al. (2004) combined traditional mark–recapture analysis with the commonly used Gompertz and Weibull models to describe senescence patterns. They found that senescence in these species can be generally described by the Gompertz model, a result likely to be of interest to researchers working on senescence in a variety of taxa. Both studies (Catchpole et al., 2004; Gaillard et al., 2004) represent useful refinements of the typical approach in senescence studies of simply fitting linear or quadratic relationships between survival and age.

Two studies addressed important methodological issues. E. Cam et al. (in press) examined the assumption of homogeneous survival probabilities when estimating recruitment to breeding status. Various studies have explored temporal variation in age of first breeding and how this co–varies with social or environmental factors, but most of these studies have ignored the size of the pool of pre–breeding individuals, most of whom are not encountered prior to actual recruitment. Methods to date have assumed no difference in pre–breeder survival among the groups of recruiting individuals being compared. Using numerical simulations, Cam et al. (in press) addressed violations of this assumption, finding that recruitment estimates can be both positively or negatively influenced by variation in pre–breeder survival, depending on circumstances, and suggest that consideration of pre–breeder survival should be taken into account in analyses of recruitment. Marshall et al. (2004) address a problem afflicting most mark–recapture studies, that of marked individuals settling beyond the boundaries of a study area and how this may affect estimates of survival. These authors simulated re–sightings of birds in areas surrounding a study "core" and found that, at least for organisms such as songbirds distributed in contiguous habitat, re–sightings in the progressively larger study plots around the core can be used to achieve relatively unbiased survival estimates. The problem addressed by Marshall et al. (2004) remains an important one, and further exploration of this issue is urgently needed.

References

- Brown, C. R. & Brown, M. B., 2004. Mark–recapture and behavioral ecology: a case study of Cliff Swallows. *Animal Biodiversity and Conservation*, 27.1: 23–34.
- Cam, E., Cooch, E. G. & Monnat, J.–Y. (in press). Earlier recruitment or earlier death? On the assumption of homogeneous survival rates in capture–recapture models to estimate recruitment. *Ecological Monographs*.
- Catchpole, E. A., Fan, Y., Morgan, B. J. T., Clutton–Brock, T. H. & Coulson, T. N., 2004. Modelling senility and dispersal of red deer. *Journal of Agricultural, Biological and Environmental Statistics*, 9: 1–26.
- Clobert, J., 1995. Capture–recapture and evolutionary ecology: a difficult wedding? *Journal of Applied Statistics*, 22: 989–1008.
- Cooch, E. G., Cam, E. & Link, W., 2002. Occam's shadow: levels of analysis in evolutionary ecology –where to next? *Journal of Applied Statistics*, 29: 19–48.
- Gaillard, J.–M., Viallefont, A., Loison, A. & Festa–Bianchet, M., 2004. Assessing senescence patterns in populations of large mammals. *Animal Biodiversity and Conservation*, 27.1: 47–58.
- Marshall, M. R., Diefenbach, D. R., Wood, L. A. & Cooper, R. J., 2004. Annual survival estimation of migratory songbirds confounded by incomplete breeding site–fidelity: study designs that may help. *Animal Biodiversity and Conservation*, 27.1: 59–72.
- Nichols, J. D. & Kendall, W. L., 1995. The use of multi–state capture–recapture models to address questions in evolutionary ecology. *Journal of Applied Statistics*, 22: 835–846.
- Reed, E. T., Gauthier, G. & Giroux, J.–F., 2004. Effects of spring conditions on breeding propensity of greater snow goose females. *Animal Biodiversity and Conservation*, 27.1: 35–46.
- Tavecchia, G., Coulson, T. N., Morgan, B. J. T., Pemberton, J. M., Pilkington, J. C., Gurland, F. M. D. & Clutton–Brock, T. H., 2005. Predictors of reproductive cost in female Soay sheep. *Journal of Animal Ecology*, 74: 201–213.