

Population dynamics of radio-marked individuals: A case study of wild turkey in the Virginias - *Russell Alpizar-Jara, Elizabeth N. Brooks, Kenneth H. Pollock, David E. Steffen, James C. Pack, and Gary W. Norman*

Wild turkey (*Meleagris gallopavo silvestris*) hunting is a popular sport in the United States, with broad regional and national significance. A 2-sex Leslie-type matrix model was developed to understand the effect of hunting on the dynamics of wild turkey populations in Virginia and West Virginia (Alpizar-Jara et al. 2001). A unique aspect of this model is that it incorporates recruitment and survival parameters derived from a large-scale radio telemetry study. About 1543 hens were radio-tagged and monitored weekly during a period of 5 years to determine causes of mortality and to estimate survival and recruitment rates (Pack et al. 1999, Norman et al. 2001). The model provides projections of population size and harvest for *Spring-Summer* and *Fall-Winter* periods, as well as information about population growth rate and age/sex structure. Deterministic and stochastic versions of the model are available online (www4.stat.ncsu.edu/~pollock/turkey/turkeymod.html) to facilitate evaluation of important hypotheses concerning turkey populations with similar structural and biological features (Brooks et al. 2002). This should enable managers to address questions related to setting seasonal harvest levels, to make comparisons among various strategies for rehabilitating declining populations and to determine appropriate harvest regulations. We illustrate how the model can be used to explore a series of hunting strategies and to evaluate the consequences of process variation in the dynamics of the population. Of particular interest is the impact of cause-specific mortality (illegal, natural and hunting) and recruitment components in the population growth rate. Our analyses show that fall hunting has the strongest negative effect on the population growth rate, and that the proportion of males in the population was more sensitive to fall rather than spring hunting.

Senescence in the great tit - *Eduardo J. Belda and Markku Orell*

Theories of ageing propose that ageing evolves as the necessary cost of processes increasing early reproductive success or because of weaker selection against late-acting mutations. They predict that the rate of ageing should increase with the increase in the intensity of age and condition independent (i.e. extrinsic) mortality. In this study we used 488 individual capture-recapture histories from a 20-year study of the great tit (*Parus major*) breeding at Oulu, northern Finland (65° N). We compared our age-specific survival pattern with results from a great tit population in southern England (52° N). Our observation of lower survival probability from age 1 to age 2 in northern Finland than in southern England suggests higher extrinsic mortality in the North. We found that in Northern Finland, the survival probability improved at age 1, remained constant at age 2 and age 3 and declined at age 4. For great tits in southern England McCleery *et al.* (1996) found senescence in the survival probability but the effect appeared at an older age (5 years). Thus, our results support the prediction from evolutionary theories that the rate of ageing should increase with the intensity of the risk of extrinsic mortality.

Daily survival probabilities of adult and juvenile cliff swallows vary with colony size and ectoparasite load - *Charles R. Brown and Mary Bomberger Brown*

One potential benefit of colonial nesting in birds is increased survival of breeding adults and/or fledged juveniles due to improved predator avoidance or better food finding in groups. The cliff swallow (*Petrochelidon pyrrhonota*) of western North America breeds in colonies ranging from a few pairs to sometimes thousands at a single site, and a number of separate costs and benefits of coloniality have been identified in this species. Yet it is unknown how these interact to affect fitness components such as survival of birds in different sized groups. Using mark-recapture data from 213 different colonies from 1983-2002 and a total sample size of 129,995 adults and 19,584 juveniles, we estimated within-season daily survival probabilities of adult and recently fledged juvenile cliff swallows at breeding colonies ranging in size from 15 to 3000 active nests at our study site in southwestern Nebraska, USA. Because transient swallows were present at some colonies, we used “age”-dependent models to estimate only the survival of resident birds. Some colonies had been fumigated to remove ectoparasitic bugs, and these allowed us to investigate the effect of ectoparasitism on daily survival. Across all years, within-season daily survival probabilities increased as colony size increased for both adults and juveniles in both fumigated and non-fumigated colonies, although the pattern was statistically stronger for fumigated colonies, and there was annual variation in the pattern among non-fumigated colonies. Birds in the parasite-free colonies had significantly higher daily survival probabilities, on average, than those occupying naturally infested colonies. The results reveal a previously unknown advantage of colonial nesting in this species, document another apparent cost of ectoparasitism, and represent the first measurement of daily adult survival during the breeding season in relation to colony size for any bird.

Applying band recovery models to an evaluation of the demographic impacts of exceptional conservation measures - *Anna M. Calvert and Gilles Gauthier*

In response to extremely rapid population growth in recent years, unusual conservation measures were implemented for greater snow geese in spring 1999 with the intention of reducing adult survival and ultimately stabilising abundance. These included the liberalisation of existing sport hunt regulations in autumn and winter and, most significantly, the initiation of a spring hunting season on staging grounds in Québec. Long-term banding and recovery data covering the periods before and after regulation changes provided us with an opportunity to evaluate the effects of these exceptional conservation measures, serving as a kind of large-scale natural experiment. We use band recovery models in MARK based on a comprehensive dataset of hunter-recovered birds (approximately 4,000 recoveries of 42,000 geese banded from 1990-2001) to determine how the changes in harvest regulations may have differentially affected age groups and sexes, and to compare the magnitude of these effects to base-line temporal variability in survival and recovery rates. Models incorporating annual harvest rate (determined independently from hunter surveys) as an external covariate are also tested in order to determine whether harvest trends interpreted from survey data accurately reflect demographic impacts. We use a simplified reporting rate estimate based on the recovery rate of radio-collared birds (assumed to be 100%) and on literature values to calculate annual hunting mortality rates from recovery rates for each component of the population, for comparison with changes in sport harvest regulations. As expected, we found an increase in recovery rates for all

age-sex groups after the initiation of conservation measures, but did not note any corresponding decline in survival rates, though this may be due to the low power of detection implicit in the use of band-recovery data. Given migratory route changes observed in the population during the period of abundance increase, we also explore different methodological options available for an evaluation of the variation in survival and recovery rates due to kill-location and season, and discuss the additional information but also the biases that arise from these analyses.

The Possible Effects of Contaminants on the Survival, Breeding Dispersal, and Natal Dispersal of Red-tailed Tropicbirds Nesting on Johnston Atoll - *Paul F. Doherty, Jr., E. A. Schreiber, Gary A. Schenk*

Annual survival and dispersal rates of adult and juvenile red-tailed tropicbirds were examined in connection with exposure to heavy metals. The incineration of a U.S. stockpile of chemical weapons stored at Johnston Atoll, in the central Pacific Ocean, exposed tropicbirds nesting in the vicinity of the plant to increased levels of human disturbance, smoke stack emissions and potential leaks. Birds nesting in this site (downwind of the plant) were compared to those nesting in a reference site (upwind of the plant) with less human disturbance, and no exposure to smoke stack emissions or other potential incineration emissions. We did not find any effect of the weapons incineration on survival of adults or juveniles between the two sites. Adult breeding dispersal rates did not differ between the sites but we did find differences in the age-specific natal dispersal rates. Birds fledged from downwind areas were less likely to return to their natal area to nest and more likely to immigrate to the upwind area than vice-versa. This asymmetry in natal dispersal rates could be caused by many factors, but we believed it is most likely due to differing vegetation densities and disturbance regimes. These results have implications for vegetation management in relation to tropicbird nest success and population size.

Assessing and Correcting for Effects of Bias on Manatee Aerial Survey Counts at the TECO Big Bend Power plant in Tampa Bay, Florida - *Holly H. Edwards, Bruce B. Ackerman, John E. Reynolds, James A. Powell and Kenneth H. Pollock*

In winter, Florida manatees (*Trichechus manatus latirostris*) aggregate in the warm-water outflows of power plants and natural springs seeking refuge from colder ambient waters temperatures. Aerial surveys that cover manatee habitat in small, well-defined areas (usually at winter aggregation sites) are useful for obtaining minimum population estimates and for assessing effects of cold weather on manatees. However, obtaining accurate population estimates from these surveys are problematic because imperfect detection is not taken into account. To identify how environmental conditions affect manatee aerial detection probability, an intensive study was conducted during winters 1999-2000 through 2002-2003 at the Tampa Electric Company's (TECO) Big Bend power plant discharge canal in Tampa Bay, Florida. Flights were flown on mostly consecutive days (4-10 days) following the passage of cold fronts. To estimate components of detection probability we marked manatees by attaching colored flags to their tail-stocks. Marked animals helped: (1) determine the overall probability of detecting manatees from the air via the use of marked animals and aerial observers (p); (2) determine the probability of detecting an animal, given that it is available to the observer using ground (p_2) and aerial observers (p_1); (3) determine the probability, from information in 1 and 2

above, of a manatee being available for observation, (p_a). Overall probability of detecting manatees for 6 surveys ranged from $p = 0.41$ to 0.83 and the probability of detection, given available, for air and ground observers ranged from $p_1 = 0.61$ to 0.75 and $p_2 = 0.60$ to 0.76 respectively. The probability of a manatee being available to the observer was $p_a = 0.46$ to 0.76 . We will use these detection probabilities to develop better population estimates for manatees.

Predicting the effect of shellfish fishery on mortality in Oystercatchers *Haematopus ostralegus* - B.J. Ens and C. Rappoldt

In the Netherlands, mechanized fishing for shellfish occurs in several intertidal areas, whose prime function is that of being a nature reserve. The fishery is hotly debated, since conservationists are convinced that declines observed in Oystercatcher populations are due to the fishermen taking away the food of the birds. To address this dispute, we developed a model that predicts how the Oystercatchers will deplete the stock of shellfish in the course of the winter. For the Oosterschelde, the first area for which we tested the model, the predicted amount of shellfish left at the end of winter coincided closely with the stock estimate of the fishery institute. The model also calculates a measure which we call food stress and which indicates the difficulty the birds experience in meeting their daily energy needs. The model does not distinguish between individuals, because we wanted to stay as close to the available measurements as possible. However, the food stress in a given year can be related to the mortality of the birds. We estimated mortality using ringing recoveries and found a close correlation between mortality and food stress. The higher the food stress during a given winter, the higher the overwinter mortality of the birds. The highest stress and overwinter mortality occurred during very cold winters when the intertidal mudflats froze over and the birds could not reach their food. We were also able to estimate the extra food stress caused by the fishery. It turns out that initially the policy of food reservation for the birds, which forbids shellfish fishery when shellfish stocks are low, did not provide sufficient guarantees for the birds. Recently, minimum stocks were set higher and preliminary calculations suggest that the new levels do provide sufficient guarantees for the birds.

Estimating Overdispersion using a Conditional Bootstrap – David Fletcher and Richard Barker

For large samples, the deviance of a mark-recapture model has a chi-squared distribution (when the model is correct). This result has led to the standard measure of overdispersion known as *c-hat*, which is the deviance divided by its degrees of freedom. In order to avoid using this large-sample approximation, Program Mark now has a parametric bootstrap procedure for estimating *c-hat*. This procedure involves generating a large number of bootstrap samples and estimating *c-hat* by dividing the observed deviance by the mean of the deviances from these samples. We suggest that this procedure should be made conditional, in the sense that we only consider bootstrap samples with the same minimal sufficient statistics as the original data. We present the results of a simulation study comparing the conditional and unconditional bootstrap procedures, focussing in particular on the coverage rates of confidence intervals for survival rates obtained using the corresponding value of *c-hat*.

What is the significance of the F parameter in combined models of live and dead encounters: site fidelity, colour-ring retention or correction for heterogeneity? - Morten Frederiksen

In the framework of the combined model of live and dead encounters of marked animals developed by Burnham (1993), the parameter denoted F is defined as an estimate of fidelity to the study area. It is obvious that if live encounters concern colour-marked individuals observed at a distance, whereas dead encounters occur irrespective of the presence of a colour-ring, F will estimate the compound probability of retaining the colour marker and remaining within the study area. However, in many studies of this type, e.g. of geese, resighting probability will not be homogeneous within the study area, resulting in sometimes pronounced resighting heterogeneity. If some animals show fidelity to locations where they are unlikely to be observed, this heterogeneity takes the form of “trap-dependence”, which in pure live-encounter studies can cause negative bias in estimated survival. How does resighting heterogeneity affect survival estimates under Burnham’s combined model?

Through a simulation study I showed that as long as dead encounters occur independently of how likely an individual is to be observed alive, Burnham’s model provides unbiased estimates of survival. Even in simulations with no permanent emigration from the study area, F is estimated as less than 1 if resightings are heterogeneous. This means that whenever resighting heterogeneity occurs in a study population, the F parameter becomes very difficult to interpret and should probably most often be regarded as a correction factor which allows unbiased estimation of survival.

Estimating true age-dependence in survival from long-lived birds only resighted as adults - Morten Frederiksen, Michael P. Harris & Sarah Wanless

In many long-lived birds with delayed recruitment, such as most seabirds, most information on survival comes from adult breeders. Pre-breeders are often more or less unobservable, and even though a proportion of marked adults may have been marked as chicks and therefore be of known age, the estimation of age-specific survival is complicated by the absence of observations during the first years of life. As a result, many published studies have used “time since first observation as breeder” as a surrogate for true age, making tests for e.g. senescent declines in survival less powerful. New developments in MARK now allow modelling of age-dependence in survival through an automatically updated individual covariate, thus obviating the need for modelling the capture history between ringing as chick and first observation as breeder.

We used this powerful approach to model age-dependence in survival of black-legged kittiwakes *Rissa tridactyla* at a North Sea colony. Although only 69 breeders were of known age (out of a total of 471 colour-ringed adults), there was strong evidence for a quadratic relationship between true age and survival, with an initial increase followed by a pronounced decline in old age. In contrast, an analysis of the complete data set using “time since first observation as breeder” as a surrogate showed a linear decline in survival with this parameter. We believe that this simple but powerful approach could be implemented for many long-lived species and could provide improved estimates of how survival changes with age, a central theme in life history theory.

Population dynamics of Starlings *Sturnus vulgaris* breeding in Britain: an integrated analysis. - *S.N. Freeman, R.A.Robinson, J.A.Clark, B.M.Griffin, S.Y.Adams and S.R.Baillie*

We describe a population model fitted to census data on the Starling at UK Common Birds Census (CBC) plots in 1965-2000. The demographic features of the model (survival and components of productivity) are calculated beforehand from national ring-recoveries and nest record data. In the most general form of the model, all parameters are assumed to vary between years, and survival rates of first-year and older birds are permitted to differ. We fit the model not to a single population index derived from the CBC data, as has been done in earlier Integrated Population Analyses of complete sets of CBC data, but to the site-based CBC counts themselves, thus better accounting for sampling covariances of annual abundance indices. Counts are assumed Poisson distributed, with expected values determined by the population model. Parameters are estimated by maximum likelihood and the method is readily applied via any Generalized Linear Modelling software.

By removing temporal fluctuations in demographic model parameters in turn, we attempt to identify which of them have the most profound influence upon changes in abundance for this species of conservation concern. It is shown that changes in mortality rates of first-year birds have probably been the major cause of the substantial national decline witnessed over this period. A regional population model however – the first constructed using CBC data for any species – suggest a greater role for adult mortality in the largely arable Eastern region, the species' UK stronghold. Population trends were similar in Northern and Western Britain, where farming is largely pastoral, and in each case changes in first-year survival remain the best candidate to explain the population changes. This difference might reflect differences in habitat availability and juvenile dispersal.

Generalized Least Square Estimators for Arnason-Schwarz Capture-Recapture Models - *Olivier Gimenez, Rémi Choquet and Jean-Dominique Lebreton*

In the analysis of multistate capture-recapture data (Williams et al., 2002, section 17.3; Lebreton and Pradel, 2003), Maximum Likelihood Estimates (Maximum Likelihood Estimates/Estimators, MLEs) are obtained by minimizing the deviance. Most often, iterative algorithms (Newton or Quasi-Newton methods; e.g., Dennis and Schnabel, 1983, sections 5 and 6) have to be used. Unfortunately, the success of this type of algorithm in reaching MLEs is frequently hampered by the presence of local minima and/or saddle points (Lebreton and Pradel, 2003).

We propose to provide classical optimization algorithms with initial values that are “good” in the sense that they belong to the attraction region of the global minimum, in order to speed up and ensure the convergence towards the global minimum (Dennis and Schnabel, 1983). To this aim, we considered first a saturated parameterization of the JMV capture-recapture model (Brownie et al., 1993), a simple generalization of the Arnason-Schwarz model, inspired by the ring-recovery models (Schwarz et al., 1993). Using the Generalized Least Squares theory (e.g., Rao, 1973, section 4i.4), we derived explicit estimates (Generalized Least Squares Estimates/Estimators, GLSEs) for the Arnason-Schwarz and other related models derived from our saturated model by linear constraints, that are asymptotically equivalent to MLEs

(Gimenez, 2003).

To illustrate our approach, GLSEs and MLEs were derived on a real example about the reproductive status of Sooty shearwaters (Scofield et al., 2001). We then performed a general evaluation of the relative merits of GLSEs in two steps: 1) based on relative bias, relative efficiency and mean square error, we performed a sequence of simulations in order to compare GLSEs and MLEs for finite sample size data sets; 2) based on six data sets from the literature, we compared the quality and the speed of convergence when initial values are a) the GLSEs for the model considered, b) default initial values in MSURGE (Choquet et al., 2003) and MARK (White and Burnham, 1999) and c) random numbers distributed uniformly over the acceptable interval for each parameter.

Although our approach - when it is used to get point estimates - seems to be overcome by the MLE, particularly in terms of precision, we advocate the use of GLSE as initial values since, regarding the examples we deal with, its direct computation speeds up and guarantees the convergence to the global minimum of the deviance.

Estimating albatross survival: dealing with unobservable states. - *Christine M. Hunter and Hal Caswell*

Survival estimation for intermittently-breeding seabirds has previously been problematic because mark-recapture methods could not account for the unobservability of non-breeding adults. New methods using multi-state mark-recapture frameworks have been proposed by Fujiwara and Caswell (2002) and Kendall and Nichols (2002) to deal with unobservable states. The estimability of relevant parameters for these models requires either extra information (e.g. by use of Pollock's robust design) or model constraints (e.g. time constancy) and has been investigated for a number of simple model structures. Here we examine a series of more complicated models that differ in the distribution of inter-breeding intervals and that distinguish between successful and failed breeders. For each model we determine sets of assumptions sufficient to make the relevant parameters estimable. Estimability of parameters for these models is of interest for many albatross species because the length of time they remain in the unobservable non-breeding state depends on the outcome of the last breeding attempt. We will identify a series of models applicable to estimating adult survival probability and inter-breeding intervals for Wandering Albatross (*Diomedea exulans*).

Estimating the chick survival of colour ringed gulls - *Risto Juvaste and Jari Valkama*

We present a method to estimate the chick survival of individually colour ringed gulls. It is based on large scale colour ringing of Herring Gulls (*Larus argentatus*) (HG) and Lesser Black-backed Gulls (*Larus fuscus*) (LBBG) in Finland during 1993-2000. Altogether 7,636 chicks of Herring Gulls and 6,045 chicks of Lesser Black-backed Gulls were ringed with individually coded colour rings (cr). By 14 February 2003, there were 42,646 sightings of 4,342 HG individuals (57%) and 21,827 sightings of 1,669 LBBG individuals (27%) in the database of Helsinki Ringing Centre. Because most of the birds were aged during ringing by measuring the wing length, the estimate for survival after ringing can be calculated from classified

percentages of total sightings. The method has been tested with HG and LBBG populations in Finland. It was found that due to the high percentage of cr-sightings, the survival of HG chicks can be estimated even in small populations. An example is a cohort of 178 chicks ringed near Lappeenranta (SE Finland), wings 55 mm-335 mm, median 200 mm. Altogether there are 370 sightings of 72 individuals from these birds. By simple analysis of cr-sightings based on linear regression we estimated that about 125 chicks fledged. The survival of chicks during the last 3-4 weeks before fledging was about 50%. By use of population analysis (Popan5/Jolly-Seber/full/birth) of the sighting data (57 sightings/37 gulls) from a nearby dump it was estimated that 104 of the fledged birds (83%) came to the dump. Estimate is however rough. Based on the yearly sightings we estimate that 24 birds (SD=5.2) were still alive in the year 2001 (Popan5/Jolly-Seber/dead only). In a similar analysis of LBBG-chicks ringed at Finnish lakes during years 1993-2000 (n=3,457) there was an unexpected decrease in survival in the group of nearly fledged chicks. The average survival decreased nearly 10% from the group 250-300 mm to the group 300-380 mm. The percentages of sightings in these groups were 54% and 45% ($\chi^2=5,9$ df=1 P=0.015 n=940). The reason for this decrease, which is against the expected trend and found in all year cohorts, will be studied by analysing the sub-cohorts, using both resightings and recoveries of metal rings.

Estimating population sizes of Herring Gulls at Joensuu dump by mark-resighting data - Risto Juvaste

The populations of Herring Gulls (*Larus argentatus*) at the rubbish dump of Joensuu were studied by population analysis based on mark-resighting data of 5,624 day-sightings of 657 colour-ringed Herring Gull individuals in the year 2000. During the breeding season the total weekly numbers of gull individuals visiting the dump were almost ten times higher than the maximum numbers of gulls seen present at any one time. The peak estimate at the end of April was over 12,000 individuals in a week (Popan5/Jolly-Seber/full). The counts of the birds present at the dump showed maximum numbers in October, when 2,000 Herring Gulls were seen at a time. However, the estimate for that week was only about 3,000 individuals. The total number of Herring Gulls visiting the Joensuu dump during the year 2000 was estimated to have been over 20,000 birds. In addition, the residence times and the timing of migration of different age groups and sub-populations of Herring Gulls were studied. The results have been used in the management of gulls at the dumps. The population dynamics of Herring Gulls at the Joensuu dump will be analysed more thoroughly by using neural computing to analyse over 50,000 cr-sightings from the years 1997 - 2003.

First use of a capture-recapture model for savannah tree demographics - G. Lahoreau, J. Gignoux and R. Julliard

Fire and grazing are the major determinants of the dynamic equilibrium between trees and grasses in African savannas. But the impact of fire on tree mortality is poorly understood. The Lamto research station in central Ivory Coast provides a model system to study the influence of fire given the relative absence of large herbivores. Since 1962, burnings have also been carried out every January, at the height of the dry season. From 1991 to 1994, demographic censuses of trees were conducted every June and December. All individuals (including seedlings) were tagged and mapped. The status of some individuals, particularly small ones, was sometimes

unknown because: (i) 10cm-high seedlings can be difficult to find in grass layers that often exceed 2m at the end of the wet season; (ii) in December, some individuals have already shed their leaves, making it impossible to judge their viability. As estimated survival rates derived only from the number of known survivors could cause bias (Lebreton, 1992), we attempted to reanalyse the data using capture-recapture models. We used the 1993 Burnham model and MARK software to estimate age/time-dependent survival of seedlings in nine tree species. Preliminary results showed up to a 4-fold increase in mortality for one-year seedlings during the dry season, presumably due to fire, with significant differences between species. The use of capture-recapture models, common used in animal populations, appears very promising to analyse this plant ecosystem.

Decomposing population growth rate: importance of adult survival, local recruitment and immigration in Willow Tits *Parus montanus* - Satu Lampila, Markku Orell, Eduardo Belda and Kari Koivula

We studied population growth rate and its components (adult survival, local juvenile survival and immigration) in Willow Tit in Northern Finland. We used capture-recapture modelling to achieve unbiased estimates of the population parameters and a components of variation analysis to partition sampling variation from process variation. During the 12-year study from 1991 to 2002 the population growth rate (λ) was close to one with considerable variation ($\bar{x} = 0.99$, coefficient of variation, $CV = 0.20$). Population projections, considering time spans of varying lengths, imply that if conditions remain as present the population is most likely declining; i.e. the impact of large variation. We used multi-strata models to uncover the relative contributions of the vital rates to λ . Adult survival had the highest contribution to the population growth rate and it was also the least variable trait studied ($\bar{x} = 0.59$, $CV = 0.067$). Partitioning the total recruitment into local juveniles and immigrants revealed that the highest contribution to the variation in λ was due to local juveniles. Indeed, the local juvenile survival was the most variable of the studied traits ($\bar{x} = 0.06$, $CV = 0.61$). Survival of willow tits after establishing in the breeding population show low temporal variation and sets the relative lower limit for population change. Thus we argue that variation in local recruitment determines the variation in λ above its relative magnitude set by adult survival. We implemented a set of *a priori* hypotheses to test if environmental factors explain the observed temporal process variation in the vital rates. Models suggested that adult survival was positively affected by pine cone abundance. However, we cannot rule out the possibility that pine cone abundance is correlated with other source of food such as invertebrates that is intensely hoarded for the upcoming winter. For juvenile survival and immigration pine cone abundance did not explain the temporal variation.

Long-term study of a king penguin population using an automatic identification system - C. Le Bohec, M. Gauthier-Clerc, J.-P. Gendner, N. Chatelain, Y. Le Maho

Birds microtagged with transponders under the skin can be identified for life and detection antennas allow the automatic identification of the birds with minimal human disturbance and presence in the field. The king penguin cycle is unusual because it lasts more than one year and birds are not synchronised in their cycle. In addition, birds that failed in their reproduction still frequent the colony throughout the year. We have employed an automatic identification setup

for the detection of the passage of free-living microtagged king penguins at Possession Island (46°25'S, 51°45'E), Crozet Archipelago. A breeding area with about 10,000 pairs is connected to the sea by three natural pathways, where antennas for bird identification were installed. From February 1998, 900 breeding adults and 1600 one-year old chicks were fitted with transponders without any external marks. Cohorts of chicks will be implanted with transponders each year.

This system allows estimation and comparison among years of variables such as arrival date for courtship, foraging trip duration at sea during incubation, brooding and winter periods, feeding frequency of chicks, duration of chick rearing, interannual return rates of adults and immatures and reproductive success. Additional studies allow determination of variation in body condition of adults, of tick parasitism and predation in relation to year and bird location in the colony. The aim of this long-term population study is to determine the reproductive strategy of these long-lived birds and the effects of age and climatic changes on their breeding performance.

AD Model Builder: A tool for fitting custom built highly parameterized nonlinear models
- Mark Maunder

AD Model Builder (ADMB, Otter Research, <http://otter-rsch.com/admodel.htm>) is becoming the predominant programming environment for producing complex, highly-parameterized fisheries stock assessment models. It has been used to fit complex nonlinear models with thousands of parameters simultaneously to multiple types of data and to fit nonlinear models with fewer parameters to hundreds of thousands of data points. ADMB is the combination of a code template and a set of libraries for C++. The code template and specific ADMB keywords reduce the amount of coding needed to implement a model. The C++ libraries supply a set of routines that are used to fit models to data. The features of ADMB include an efficient function minimizer, a MCMC algorithm for Bayesian integration, matrix algebra, automated likelihood profiles, parallel processing, and random effects parameters. ADMB uses automatic differentiation for exact derivatives, which makes the minimization procedure more efficient and stable than other packages that use finite difference approximation. ADMB provides a flexible stepwise process to sequentially estimate the parameters, and allows the placing of bounds on all estimated parameters that restrict the range of possible parameter values. The MCMC algorithm implemented in ADMB has jumping rules that are based on the variance-covariance estimates at the mode of the posterior distribution and starts at the mode of that distribution, which makes the algorithm more efficient (*i.e.* reduces the burn-in time). Random-effect parameters are implemented with Laplace's approximation with automatic second derivatives. All the underlying code used to define the model and objective function is coded in C++ (mainly C). Therefore, ADMB is very flexible, and is useful for custom-built models. ADMB includes parallel processing to make computationally intense models more practical.

Use of log-linear models to analyse habitat selection of individually marked song thrushes
Turdus philomelos - Will J. Peach

Understanding habitat utilisation and selection patterns at different scales continues to be a fundamental objective of many applied biologists. Compositional analysis (Aebischer et al., 1993, Ecology 74, 131-1325) is now widely used but can be problematic to implement when habitats are not available within some home ranges. Log-linear models offer great flexibility in

analysing habitat selection data and testing covariate effects (Manley et al. 1993, Resource Selection by Animals. Chapman & Hall; Green et al. 2000, J. Zool. 250, 161-184) but have not been widely adopted by biologists. Here I use log-linear models to analyse habitat selection patterns of radio-tagged song thrushes *Turdus philomelos*, a species that is red-listed in the UK following a population decline of approximately 70%. Thrushes were located during two successive breeding seasons in two farmland populations – one stable and one rapidly declining. Four thousand fixes were available from 86 tagged individuals. We used log-linear models to analyse variation in fix density across habitats. The model accounted for differences in ranging behaviour between nesting and non-nesting periods and in the numbers of available fixes per individual. It also tested the influence of a range of potential covariates on the pattern of fix density including tag attachment method, year, season, landscape and study area. Randomisation tests in which the individual bird was the unit of replication were used to assess statistical significance. Fix density varied significantly across habitats but not between study areas or any of the other covariates. Large differences in habitat utilisation between study areas mainly reflect differences in habitat availability. Numerical problems arose when there are no fixes in one covariate level. Log-linear models provide an efficient and flexible means of analysing habitat selection data. There is a pressing need to compare the performance of compositional analysis and log-linear models, and to develop user-friendly software that includes randomisation significance testing and the testing of covariate effects.

Demographic mechanisms of the population decline of the song thrush *Turdus philomelos* in Britain - RA Robinson, R E Green, S R Baillie & W J Peach

In Britain, the song thrush *Turdus philomelos* is categorized as a species of high national conservation concern because of a large population decline during the last three decades. We used survey data to calculate a series of annual national population estimates for woodland and farmland habitats combined for the period 1964-2000. We then used turning points analysis to identify seven blocks of years within the period of decline (1968-2000) with uniform rates of population change in the smoothed trend. Six of the seven blocks showed declines.

We used recoveries of song thrushes ringed by participants in the national ringing scheme as nestlings, juveniles and adults in April-September to estimate survival rates and modeled survival rates separately for the post-fledging period, the remainder of the first year and for adults. Daily survival probability was much lower during the post-fledging period than in the remainder of the first year or for older birds. There was evidence of variation in survival rates among blocks of years with different rates of population change and in particular for first year survival. There were significant positive correlations across blocks between mean population multiplication rate and both post fledging and first year survival.

The demographic mechanism underlying the song thrush population decline appears to be changes in survival in the first year and perhaps also the post-fledging period. The environmental causes of these changes in survival are not known. Adverse weather conditions contributed, but were not sufficient on their own. Changes in farming practice, land drainage, pesticides and changes in predator numbers are all candidates.

Estimating demographic contributions to population growth and decline in a salamander:

a multistate model with a unobservable state - Benedikt R. Schmidt, Rainer Feldmann, Michael Schaub

Amphibian populations are declining worldwide. The reasons for the declines and the factors that govern population dynamics are poorly understood. Efficient conservation action requires that we understand which stage(s) in the complex life cycle contribute most to population growth (or decline) and which stage(s) are most sensitive to environmental change. Here, we study the demography of a stationary and a declining population (based on unadjusted counts) of the salamander *Salamandra salamandra*, and assess whether an observed decline in one population is due to a change in recruitment or adult survival. The two populations were studied for c. 20 years and all salamanders were known individually. We use a multistate capture-mark-recapture model with an unobservable state to estimate both recruitment and adult survival probabilities. Our analysis shows constant adult survival in the stationary population, and declining adult survival and constant recruitment in the declining population. The analysis also shows that the population growth rate of the declining population was not only negative but also steadily decreasing. The results suggest that the population decline is due to a change in adult survival, which was probably caused by a change in forest management. Our results provide a counterexample to the usual paradigm in amphibian population ecology, which states that population growth is determined at the larval stage. Our analysis also highlights the value of capture-mark-recapture analysis for understanding population dynamics and decline.

Toll-free bands and erroneous reporting behavior: effects on survival estimation - Joel A. Schmutz

Previous simulation study by Anderson and Burnham (1980) examined the bias in survival estimation when there is a "delay" in the reporting of bands - that is, reporting bands with an erroneous and later recovery date than when they were truly recovered. Their conclusion was that the bias was small and negligible compared to the precision of estimates. Recent analyses of band recovery data from Greater White-fronted Geese suggest that bias may exceed 5%, and this large and biologically relevant level of bias may be exacerbated by the advent of band reporting using toll-free telephone numbers. Specifically, when analyzing recoveries of birds banded during 1990-1995, estimated survival rates were approximately 5% greater when using recoveries through 2000 (a "non-triangular" data matrix, where years of recovery exceed years of banding) than when using recoveries through 1995 (a "triangular" data matrix). Broad scale toll-free band reporting started in 1996, and I hypothesized that many previously recovered but unreported bands would now get reported by this new toll-free system, and importantly, that many would be reported with an inaccurate year of recovery. Data simulations using hypothesized amounts of single and multi-year "delay" in reporting were able to replicate the results seen with the Greater White-fronted Geese. Band recovery data from other waterfowl also demonstrated this pattern. The bias induced by this reporting process is expected to be greater in non-triangular than in triangular data sets. Comparing results from triangular vs. non-triangular data sets over a long time period will elucidate whether bias from this band reporting behavior is relegated just to the advent of toll-free band reporting or, alternatively, it has been a long term source of bias in band recovery data sets.

On the use of Capture-Recapture data in parameterising a Population Viability Analysis model for the Bog Fritillary butterfly - *Nicolas Schtickzelle* and *Michel Baguette*

In the context of a species-based conservation strategy, Population Viability Analysis (PVA) is used to determine the habitat network configuration ensuring the highest persistence of a species in a given landscape. Structured population models taking local population dynamics into account are effective tools for the conservation of threatened species at the very end of the fragmentation process. Nevertheless, they require estimates of various parameters at the population level, which may be obtained from capture-recapture data.

This poster details how Capture-Recapture data have been used to parameterise a PVA model designed for a viability analysis of the Bog Fritillary butterfly (*Proclossiana eunomia*). The study system is a metapopulation located in a highly fragmented landscape in southern Belgium, where this butterfly is used as a surrogate species for wet meadow communities. This metapopulation consists of 20 suitable habitat patches spread on 6 km along the Lienne river.

Daily Capture-Recapture data during 10 generations provided information to estimate the following parameters:

- Survival, catchability, recruitment, daily and total (per generation) population size were obtained by live-recapture CJS and JS models, fitted using MARK (White & Burnham 1999) and POPAN (Arnason & Schwarz 1999) software respectively. The sequence of population sizes during the 10 generations was used to derive estimates of density dependence parameters (maximum population growth rate and carrying capacity) as well as the magnitude of environmental stochasticity (yearly variation of population growth rate).
- Dispersal parameters (emigration according to patch area and dispersal probability according to patch connectivity) were estimated using the Virtual Migration model (Hanski *et al.* 2000).
- Spatial correlation of local population dynamics as a function of between-populations distance was determined using yearly frequentation of individual habitat patches by butterflies as reflected by number of captures.

Demographic mechanisms of density dependence in Black Brant - *James S. Sedinger*

Density dependence in long-lived vertebrates is typically manifested in reduced recruitment of young, while adult survival is preserved. The Black Brant population breeding in western Alaska declined substantially during the late 1970s and early 1980s. Coworkers and I have studied Black Brant breeding at the Tutakoke River colony on the Bering Sea coast of Alaska since 1984. During the study more than 40,000 individuals have been marked with uniquely coded plastic leg bands. Using observations and captures of individuals on the breeding colony, at other breeding locations, and on wintering estuaries in Mexico, we have monitored a number of demographic parameters as the population increased to near historic levels. Consistent with general patterns for other long-lived vertebrates, adult survival did not decline during the period of population increase. We detected no density-related effects on breeding probability, based on robust design. Using a variant of Burnham models we did not detect any density-related variation in dispersal rates. Growth rates of young declined during population increase, which was associated with declines in first-year survival. There were additional density-related effects

on survival, as evidenced by the fact that survival in more recent cohorts declined more than would be expected based on gosling size alone. Overall, we found no change in adult survival or reproductive investment by adults but we did find reduced recruitment at higher population densities.

Relationships between landscape characteristics and duck nesting success in the Missouri Coteau region of North Dakota - *Scott E. Stephens, Jay J. Rotella, Mark S. Lindberg, and Mark L. Taper*

For upland-nesting dabbling ducks, nesting success is the primary determinant of population growth rates. As a result, a great deal of activity is focused on understanding factors related to nesting success rates and most conservation programs seek to affect nesting success rates. We developed models to understand and explain variation in nesting success rates across a gradient of landscape types in the Missouri Coteau region of North Dakota. Ultimately, our goal was to develop statistical models that could be utilized in spatially explicit habitat models to guide strategic targeting of conservation programs across broad spatial scales. During 2000-2002, we collected data on the fates of over 5,000 duck nests from 18 study sites. We developed *a priori* models that represented various hypotheses about how landscape-, patch-, and nest-level habitat covariates influence nest survival. Because of the scale-dependent nature of landscape-scale metrics, we measured landscape covariates at 5 spatial extents (i.e., 10.4, 23.3, 41.4, 64.7 and 93.2 square km). We also took advantage of variance components methods to estimate the amount of spatial process variation in nesting success rates. Based on the results of our *a priori* models, we examined a limited number of exploratory models. Our best models included only landscape-level habitat covariates such as the amount of grassland, grassland edge and wetland density. Additionally, models that measured landscape metrics at multiple spatial scales were dramatically better (ΔAIC 32.3) than models that measured all landscape metrics at the same landscape scale. We estimate that the landscape covariates in our best model captured 90% of spatial process variation in nesting success in our dataset. Thus, our statistical model looks to hold great utility for use in spatially explicit landscape models to guide conservation programs. We suggest that avian researchers interested in relationships between demographic rates and habitat characteristics measure landscape variables at multiple landscape scales to determine which scales are most relevant.

A unified framework for modelling wildlife population dynamics - *Len Thomas, Stephen T. Buckland, Ken B. Newman and John Harwood*

We propose a unified framework for defining and fitting stochastic, discrete time, discrete stage population dynamics models. The biological system is described by a state-space model, where the true but unknown state of the population is modelled in a state process, and this is linked to survey data by an observation process. All sources of uncertainty in the inputs, including uncertainty about model specification, are readily incorporated. We show how the state process can be represented as a generalization of the standard Leslie or Lefkovitch matrix. By dividing the state process into sub-processes, complex models can be easily constructed from manageable building blocks. We illustrate the approach with a model of the British grey seal metapopulation. We use Bayesian sequential importance sampling with kernel smoothing to fit the model.

Profile likelihood intervals: a new feature of program MARK to solve a problem of "standard theory" - *Gary C. White and Kenneth P. Burnham*

If the MLE of a parameter (such as a survival probability) lies on, or too near to, the boundary of a parameter space then what people are taught as large sample (i.e., standard) frequentist theory for obtaining an estimated standard error and confidence interval can fail abysmally. There is for this situation a good non-Bayesian solution for obtaining a confidence interval: the profile likelihood interval. We will give an explanation of this interval; how it is computed in MARK will be noted. There is also the Bayesian credibility interval as a solution. Under a uniform prior on a probability parameter the two intervals are very similar. We use the classical female blackneed capsids data to give examples of different confidence intervals for survival probabilities (S), with or without the constraint $S \leq 1$: MLE with large sample standard errors and classical intervals (the MARK default), pure likelihood, and inference from the Bayesian posterior from MCMC data analysis.