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JOINT ANALYSIS OF LIVE AND DEAD ENCOUNTERS OF MARKED ANIMALS

RICHARD J. BARKER

Department of Mathematics and Statistics, University of Otago, P.O. Box 56, Dunedin, New Zealand, rbarker@maths.otago.ac.nz

GARY C. WHITE

Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523, USA

Abstract: Recently developed methods for analyzing mark–recapture data allow simultaneous modeling of information from a variety of animal encounters. Incorporating this extra information in an analysis requires use of a more complicated model but can lead to improved precision of estimates. An important aspect of such joint models is that movement of animals to and from the banding site can be incorporated. This allows relaxation of a restrictive assumption made about animal movement in the Cormack–Jolly–Seber model. We review the theory behind joint analysis of mark–recapture data and illustrate application of the models using data from mallard ducks (*Anas platyrhynchos*), paradise shelducks (*Tadorna variegata*), and common goldeneye ducks (*Bucephala clangula*).

Key words: band recovery, common goldeneye duck, mallard duck, mark–recapture, mark–resight, paradise shelduck, site fidelity, temporary emigration

Reliable decision-making on the management and conservation of biological populations depends on the availability of good information. Knowledge of survival probabilities in particular is needed as an indicator of population status and to understand population dynamics (Caughley 1977, Lebreton et al. 1992, Clobert 1995). Survival probabilities are typically estimated using mark–recapture studies, but these studies usually require a substantial commitment of time and money to generate reliable data. Moreover, data in mark–recapture studies are obtained through re-encounters of marked animals following release, but the number and type of re-encounters is not directly controlled by the researcher. Instead, recapture data represent the outcome of random recapture and tag-recovery processes.

Following release, information may be provided by marked animals in 3 ways: (1) live-recapture of animals during marking operations; (2) recovery of marks from animals found dead between marking occasions; and (3) reported sightings (alive) of marked animals

between marking occasions. Most studies are designed so that just 1 type of data provides the primary information for the construction of a mark–recapture model. However, these multiple sources of information on marked animals can be exploited in the analysis phase of the study to increase precision of key parameter estimates (Catchpole et al. 1998) and to relax assumptions.

Historically, 2 distinct models have dominated analyses of mark–recapture data for open animal populations. First is the Jolly–Seber (JS) model (Jolly 1965, Seber 1965), used to estimate abundance, or the Cormack–Jolly–Seber (CJS) model, used in survival probabilities only (Cormack 1964). In the JS and CJS models, data are obtained from the recapture of marked animals at subsequent marking or recapture occasions. These activities may be either the live-recapture of animals during trapping operations or live resightings over a short time period during which the population is assumed closed. An important assumption of the JS model is that if animals leave the study population, they do so permanently. Under this assumption, the JS survival probability is a confounded parameter representing the joint probability that the animal survived and did not emigrate between sampling times i and $i+1$.

Permanent emigration is often listed as an assumption for the CJS model; however Burnham (1993) has shown that in the CJS model permanent emigration is indistinguishable from random emigration. Under random emigration, an animal may leave the population segment where it is at risk of capture and later return. However, the probability that the animal is at risk of capture on a particular marking occasion does not depend on whether it was at risk of capture on earlier marking occasions. Under random emigration, the CJS survival parameter represents a true survival rate and the capture probability and movement probabilities are confounded (Burnham 1993).

The second major type of mark–recapture model arises as an important restricted version of the CJS model and is appropriate when recaptures of marked animals are obtained through recovery of dead animals. These so-called band recovery models (Brownie et al. 1978, 1985) allow encounters of dead animals (band recoveries) to occur continuously through time and throughout the study area. Regular releases of marked animals must be made during the study so that survival probabilities can be estimated. The process of trapping new animals for marking provides opportunities for recapturing previously marked animals.

Live-recaptures in band recovery studies have traditionally been ignored, partly because of the apparent technical difficulties in simultaneously modeling the 2 data types and partly because in many band recovery studies, live-recapture during trapping has been uncommon. In some studies, the number of live recaptures may be substantial. This is true for relatively sedentary animal populations such as New Zealand waterfowl.

This situation was anticipated by Jolly (1965:239) when he considered his solutions to the JS model. He suggested that the recapture statistics used in the capture and survival probability estimators be augmented by resightings of animals obtained between capture occasions. Buckland (1980) adopted this suggestion in his modified analysis to incorporate recoveries of dead animals, however, except for Buckland's article there has been little follow-up to Jolly's (1965) suggestion.

Mardekian and McDonald (1981) proposed a method for analyzing joint band-recovery and live-recapture data that exploited the modeling approach and computer programs of Brownie et al. (1978, 1985). To avoid complicated modeling of the encounter history, Mardekian and McDonald (1981) ignored intermediate recapture data and instead modeled the last known fate of each released animal. Although simple, this method of analysis is inefficient because it ignores intermediate captures.

Recently Burnham (1993) developed a formal model for the joint analysis of live-recapture and ring-recovery data when all animals in the study are exposed to both types of sampling. This model was extended by Catchpole et al. (1998) to allow age- and time-dependent parameters. Szymczak and Rexstad (1991) used Burnham's model to estimate survival and site fidelity probabilities of a gadwall (*Anas strepera*) population. Barker (1995, 1997) generalized Burnham's (1993) model to include information from resightings of live animals obtained between marking occasions. This model extends the resighting models of Cormack (1964) and Brownie and Robson (1983) to allow resighting to occur any time between marking occasions as well as including live-recapture and dead-recovery data. Interestingly, Jolly's (1965) earlier suggestion for augmenting live-recapture data with resightings leads to the maximum likelihood estimators for capture and survival probabilities, but only under the assumption of no, or random, emigration (Barker 1997).

Here, we review the key issues and ideas involving joint analysis of mark-recapture data with several types of re-encounter. Data from banding studies of mallard ducks, paradise shelducks, and common goldeneye ducks are used for illustration.

DATA STRUCTURE AND MODELING

Depending on the re-encounter mechanisms operating, possible survival and re-encounter events following release at time i and up until time $i+1$ can be summarized as follows:

- the animal may die with no encounter (alive or dead) following release;
- the animal may die without being resighted prior to death, but be found after death;
- the animal may be resighted alive, then die and be found after death;
- the animal may survive the interval without being resighted and avoid capture at $i+1$;

- the animal may survive the interval without being resighted and be caught at $i+1$;
- the animal may survive the interval and be resighted alive during the interval but avoid capture at $i+1$;
- the animal may survive the interval and be resighted alive during the interval resighted and be caught at $i+1$.

The raw data can be expressed using the encounter history format adopted for program MARK (White and Burnham 1999) where a pair of indicator variables (LD) are defined for each encounter period. The L member of the i th pair is used to indicate whether or not the animal was captured at the i th trapping occasion and can take the value 0, meaning the animal was not captured, or 1 if the animal was captured. The D member of the i th pair is used to specify live or dead encounters between trapping sessions. D is assigned the value 0 if the animal was not encountered during the interval. If D has the value 1, this means the animal was reported dead during the interval. D has the value 2 if the animal was resighted alive during the interval. It is possible for an animal to be resighted alive during an interval and then be found dead later in that same interval. In such cases, the earlier live resightings in the interval are ignored without loss of efficiency and D is given the value 1.

For example, consider an animal in a 5-period study that has the encounter history 10101002. This tells us that it was captured on the first occasion, and recaptured again on the second, third, and fourth occasions. It was not captured on the fifth occasion, but was seen alive during the last interval. As shown in this example, there can be multiple occasions with a 1 in the L columns. A 2 may also appear several times in the D columns, but only 1 D column can have a 1, since subsequent encounters are not possible because the animal was found dead. Finally, each encounter history also has a weighting variable used to denote the number of animals with that history. Animals removed from the population at capture are given a negative weight.

Parameters

The focus of our modeling is animal survival and we do not consider estimating abundance or recruitment parameters. Parameters and their definitions are as follows:

S_i = The probability an animal alive at time i is alive at time $i+1$.

P_i = The probability an animal at risk of capture at trapping occasion i is captured.

r_i = The probability a marked animal that dies in $i, i+1$ is found and its band reported.

R_i = The probability that a marked animal alive at $i+1$ is resighted alive between i and $i+1$.

R_i^c = The probability that a marked animal that dies in $i, i+1$ is resighted alive in this interval before it died.

F_i = The probability that an animal at risk of capture at time i is again at risk of capture at time $i+1$.

$F\zeta$ = The probability that an animal not at risk of capture at time i is at risk of capture at time $i+1$.

The full model is an extension of Burnham's (1993) live/dead model and allows live resightings to be reported any time during the open period between live recapture occasions. Using program MARK, the model can easily be generalized to incorporate age- and group-effects and to include individual covariates (White and Burnham 1999). Parameter estimates are obtained by maximizing the likelihood function constructed from the probabilities of each distinct encounter history. For details, see Barker (1995).

Animal Movement

An important feature of mark-recapture studies is that a researcher can only capture animals associated with the trapping site. Furthermore, there is usually little control over exactly which animals are at risk of capture, and animals available for capture in 1 trapping session may not be available for trapping in other sessions.

The Jolly-Seber model assumes that animal migration is permanent (Seber 1982), meaning that if an animal leaves the at-risk-of-capture component of the population, then it is not permitted to return. In many studies, such an assumption may be hard to justify, and movement of animals both in and out of the trapping site may occur. Therefore, it is important that analyses be flexible enough to allow other types of animal movement.

Random emigration (Burnham 1993) occurs if the risk of capture at i for animals in the population at $i-1$ is the same for all animals. It is just 1 possible type of movement in and out of the study site. A more general model considered by Kendall et al. (1995) in the context of Pollock's robust design (Pollock 1982) is Markov movement, where the probability an animal is at risk of capture at time i depends on whether it was at risk of capture at time $i-1$. Permanent emigration is a special case of Markov emigration where the probability of subsequent capture is 0 for animals not at risk of capture at i . Generalizations of the Markov emigration model also can be envisaged that allow dependence to extend for more than 1 time period, for example, the memory model of Brownie et al. (1993).

Under Markov emigration, animals that are at risk of capture at time i leave the study area with probability $(1 - F_i)$. Thus, F_i has the same interpretation as in Burnham's (1993) live-dead model as the fidelity to the study area. Animals not at risk of capture are permitted to return to the study area with probability F'_i . (The definition we have for F'_i is different from that used by Barker [1997]. The definition adopted in this article is consistent with the definition used by Kendall et al. [1995].) Restrictions on the movement parameters used to define random and permanent emigration are given in Table 1 along with other constraints that can be used to define most standard mark-recapture models.

To illustrate the meaning of the emigration parameters, suppose an animal is captured during the first

Table 1. Constraints incorporated in the joint model in program MARK for live recaptures, live resightings, and dead recoveries to generate some standard mark-recapture models and restrictions on allowable animal movement.

Constraints	Model
$F\zeta = 0$	Permanent emigration
$F_i = 1, F\zeta = 0^a$	Random emigration
$R_i = R'_i = 0, F\zeta = 0$	Burnham's (1993) model under permanent emigration
$R_i = R'_i = 0, F_i = 1, F\zeta = 0$	Burnham's (1993) model under random emigration
$r_i = R_i = R'_i = 0, F_i = 1, F\zeta = 0$	Cormack-Jolly-Seber model
$p_i = 0, R_i = R'_i = 0, F_i = 1, F\zeta = 0$	Model M1 of Brownie et al. (1985)

^a The constraint $F\zeta = 0$ here is arbitrary as $F\zeta$ does not contribute to the likelihood function if $F_i = 1$.

trapping session, not captured during the second trapping session, and then captured during the third trapping session. Given that the animal was alive at time 3 we can write the probability as

$$[(1 - F_1)F\zeta_2 + F_1(1 - p_2)F_2]p_3.$$

The term in square brackets represents the probability that the animal was not captured during the second trapping session but was at risk of capture at time 3. The first product within the brackets, $(1 - F_1)F\zeta_2$, is the joint probability that the animal emigrated between the first 2 trapping sessions (with probability $1 - F_1$) and then immigrated back onto the study area during the interval between the second and third trapping sessions (with probability $F\zeta_2$). However, a second possibility exists for why the animal was not captured—it could have remained in the study area and not been captured. The term F_1 represents the probability that it remained on the study area between time 1 and 2 and the term $(1 - p_2)$ is the probability that it was not captured at time 2. The final term F_2 represents the probability that the animal remained on the study area so that it was available for capture during the third trapping session.

Under Markov emigration, many of the movement parameters are confounded, although program MARK will correctly find the maximum of the likelihood function. Usually, it also correctly computes the number of estimable parameters. A version of the Markov emigration model in which movement parameters are estimable is where movement probabilities are constrained through time. That is, $F_1 = F_2 = \dots = F_{t-1} = F$ and $F\zeta_1 = F\zeta_2 = \dots = F\zeta_{t-2} = F\zeta$. Even with these constraints, the Markov emigration model may perform poorly. In

practice, good estimates of the parameters F and F' can be obtained if there is a large difference between F and F' .

EXAMPLES

Mallard Ducks

Mallard ducks were banded at sites in the Manawatu Region of the North Island, New Zealand, by the Wellington Fish and Game Council between 1986 and 1990. The primary source of re-encounter data is from band recoveries up until 1990 obtained during the May–July duck hunting season. However, recaptures of animals during February banding operations are also available.

We first analyzed the data using the joint model developed by Burnham (1993) expanded to include age and sex effects on parameters. In addition, the reporting probability for a bird in year i depended on whether or not the bird was also captured (initial capture or recapture) during the trapping operation in year i . This model generalizes model M0 of Brownie et al. (1985) in which recovery rate differed for birds in their first year following banding. Brownie et al. (1985) argued that this model would be useful in situations where band-reporting rate is different near the banding site. In their model, this affects only newly banded birds. However, in our study, the reporting rate associated with the banding site in a particular year should also apply to previously marked birds that were recaptured, because they are also known to be associated with the banding site in that year.

The goodness-of-fit for this model was assessed using a parametric bootstrap procedure available in program MARK in which the deviance is compared to randomly generated values obtained from the fitted model. If a small (e.g., < 0.05) proportion of simulated values are larger than the observed value, then this provides evidence that the model fits the data poorly. This test provided strong evidence that the model failed to represent the data adequately ($P < 0.001$). To try to account for this lack of fit, we generalized the model to allow Markov emigration with different time-specific parameters for each age and sex class, and in the case of adults, reporting rate class. However, this model also showed strong evidence of lack of fit ($P < 0.002$). Accordingly, unless otherwise stated, model selection was based on a quasi-likelihood corrected version of Akaike's Information Criterion ($QAIC_c$) (White et al. 2001).

Using a likelihood ratio test (Cox and Hinkley 1974), there was no evidence that the Markov emigration model offered significant improvement over permanent emigration, so we used the permanent emigration model with all parameters time-dependent as a starting point for analysis. We then fitted a series of reduced parameter models with varying restrictions on the nature of age, sex, and time dependency on the 4 parameters.

The model minimizing $QAIC_c$ had a sex-dependent survival probability that was the same for each age and year, and a time-dependent capture probability that was the same for each age and sex. The logit of the reporting rate followed a linear trend in time with 6 distinct parallel trend lines, 1 for each combination of age and sex with adults further categorized according to whether the reporting rate was for a year in which the animal had been captured. Finally, there was a different value for site fidelity probabilities for each combination of age and time, but the site fidelity parameter varied in parallel for the 2 sexes on the logit scale.

Parameter estimates for this model indicated the following:

- male survival probabilities ($\hat{S} = 0.533$, $SE = 0.034$) were higher than for females ($\hat{S} = 0.465$, $SE = 0.029$);
- the odds of band reporting were estimated as 1.335 (95% CI = 1.045, 1.705) times higher for adults captured in the current year than adults not captured;
- the odds of band reporting were estimated as 1.844 (95% CI = 1.579, 2.153) times higher for juveniles than adults in their first year following a capture or recapture;
- the odds of band reporting for males was estimated as 1.304 (95% CI = 1.112, 1.527) times higher than for females;
- the odds of band reporting declined at an estimated rate of 8.8% (95% CI = 3.4%, 14.4%) per year during the study;
- juveniles were less faithful to the banding site than adults in all years, and females were more faithful with the odds of the bird remaining faithful to the banding site 2.895 (95% CI = 1.822, 4.599) times higher for females than males.

To compare estimates of survival rate with those obtained under a standard band recovery analysis, we fitted the same model in program MARK using an age-specific band reporting probability but ignoring live recaptures (hence, there are no recapture or site fidelity parameters in this model). Under the band-recovery model, the male survival probability was estimated as $\hat{S} = 0.536$ ($SE = 0.046$), and the female survival probability was estimated as $\hat{S} = 0.430$ ($SE = 0.046$). Therefore, under the joint live-recapture/dead-recovery model, standard errors of the survival rate were 74% of the value for males, and 58% of the value for females obtained under the band-recovery model.

Paradise Shelduck

Paradise shelduck were banded 1987–1990 in the Wanganui District of the North Island, New Zealand. Molting concentrations were trapped in January each year from 1988 to 1990 with recaptures of animals during banding operations as the primary source of re-encounters. In addition, bands were recovered by waterfowl hunters during the May–August paradise shelduck hunting seasons.

An initial analysis was carried out by fitting the model $S(t) p(t) r(t^*f) F(t) F(t)$ (time-dependent Markov

emigration model) in which survival, capture, and movement probabilities are all time-specific, and where the reporting probability for time i depends on whether the bird was caught at time i . The parametric, bootstrap, goodness-of-fit test provided evidence that the model failed to represent the data adequately ($P = 0.016$); therefore, model selection was based on QAIC_c.

To select a more parsimonious model, we fitted a series of reduced parameter models using $S(t) p(t) r(t^{*f}) F(t) F(\cdot) F'(\cdot) = 0$ (permanent emigration with no time variation in site fidelity) or $S(t) p(t) r(t^{*f}) F(\cdot) F'(\cdot)$ (Markov emigration with no time variation in movement probabilities). The difference in QAIC_c between these 2 models was 1.28, which indicates there is little to distinguish between them (Burnham and Anderson 1998).

Using likelihood ratio tests, there was evidence of time variation in reporting rates ($\chi^2_{10} = 20.073$, $P = 0.029$) and very strong evidence that reporting rates for birds captured or recaptured in January were different than those not captured ($\chi^2_4 = 36.691$, $P < 0.001$). For both models and in each of 1987, 1988, and 1989 (reporting and survival parameters for 1990 are confounded), birds that were captured or recaptured at the banding site in January were more likely to be shot and have their band reported than birds that were not captured. There was also evidence that this difference varied between years ($\chi^2_3 = 10.152$, $P = 0.017$).

Capture probabilities appeared to vary between sampling occasions ($\chi^2_1 = 9.052$, $P = 0.003$), but there was no evidence that movement probabilities varied between sampling occasions ($P = 0.248$). Although a comparison of the models $S(t) p(t) r(t^{*f}) F(t) F(\cdot) F'(\cdot)$ and $S(\cdot) p(\cdot) r(t^{*f}) F(t) F(\cdot) F'(\cdot)$ provided no evidence that survival rates varied through time ($P = 0.136$), there was strong evidence of time variation in survival probabilities after removing time variation in the movement probabilities ($\chi^2_3 = 11.617$, $P = 0.009$).

Under the model $S(t) p(t) r(t^{*f}) F(\cdot) F'(\cdot)$, the estimated probability a bird was at a trapped molt site in year i was 0.671 (SE = 0.084) if the bird was at a trapped molt site in year $i-1$, but only 0.074 (SE = 0.073) if the bird was not at a trapped molt site in year $i-1$. Therefore, although birds tend to remain at the same location each year there is some movement, and birds are more likely to move away from a trapped molt site than move to a trapped site.

Common Goldeneye Ducks

Female common goldeneye ducks were trapped in nest boxes near Preetz in the Schleswig-Holstein District of Germany between 1988 and 1997. Recaptures of nesting females were obtained during nestbox searches, and live resightings of banded birds were reported by members of the public. To make full use of available information, these activities need to be analyzed using

a joint live-recapture/live-resighting model. The first model we fitted to these data was $S(t) p(t) r(t) R(t) R(\cdot) F(t) F(\cdot)$, in which all parameters are time specific. For this model, there was no evidence that the model did not fit the data using a bootstrap goodness-of-fit test ($P = 0.628$).

After fitting a series of reduced parameter models, the best model appeared to be $S(\cdot) p(\cdot) r(\cdot) R(t) R(\cdot) F(\cdot) F(\cdot)$ in which survival, recapture, reporting, and movement probabilities are constant through time and where the resighting parameters are time dependent, but with R_i equal to R_j for each time period. Note that in this model, resighting probabilities are not influenced by whether or not the animal survives the resighting period. The model makes sense only if the population is closed during the resighting period. Because almost all resighting effort took place during the summer breeding season and the survival probability is high ($S = 0.804$, SE = 0.023), the assumption that $R_i = R_j$ in each period is reasonable in this study.

Using likelihood ratio tests, there was weak evidence of time-dependent survival rates ($\chi^2_8 = 14.034$, $P = 0.081$), which suggests that a useful intermediate model between the time-invariant and time-varying models might be a model where time variation is modeled as a random effect (White et al. 2001).

There was strong evidence against the permanent ($\chi^2_8 = 26.062$, $P = 0.001$) and random ($\chi^2_{17} = 41.531$, $P = 0.001$) emigration models, but no evidence that movement probabilities under the Markov model varied through time ($\chi^2_{13} = 15.193$, $P = 0.296$). Under the model $S(\cdot) p(\cdot) r(\cdot) R(t) R(\cdot) F(\cdot) F(\cdot)$, the probability of being at a sampled nest box in year i was 0.886 (SE = 0.039) if the bird was at a sampled nest box in year $i-1$, and 0.154 (SE = 0.084) if the bird was not at a sampled nest box in year $i-1$. Therefore, birds tended to remain in the same subpopulation from year to year, with the probability of remaining about the same for the 2 subpopulations.

DISCUSSION

By taking advantage of multiple information sources, estimates of key wildlife population parameters obtained from mark-recapture data can be improved in several important ways. First, the inclusion of the extra information can lead to considerable improvement in precision of parameter estimates. Despite the need for additional complexity in the model, it can be shown that expanding a model to incorporate extra information reduces the sampling variances of the parameters of interest (R. J. Barker and L. Kavalieris, unpublished data). This is most evident in the mallard duck, band-recovery analysis where including information from live-recaptures reduced standard errors of the survival rate estimates by 25% for males and 37% for females. Similar improvements in precision in a standard band-recovery analysis require about a 2-fold increase in sampling effort.

The second advantage of joint models is that they allow relaxation of some assumptions. For example, the assumption of permanent or random emigration in a study based on live recaptures can be relaxed if live resightings or dead recoveries are included in the analysis. Nonrandom temporary emigration may be an important source of lack of fit in many analyses and was apparent in the common goldeneye study and possibly in the paradise shelduck study. In each case, the movement probability estimates indicated a degree of fidelity to the location the birds occupied in successive years. Birds at risk of capture in year i were more likely to be at risk of capture in year $i+1$ than birds that were not at risk of capture in year i . Finally, mark loss is another potential problem in mark-recapture studies (Nelson et al. 1980). In band-recovery studies, incorporating live recaptures into the analysis provides potential for modeling band loss if a double-marking scheme, preferably involving permanent marks, is used (Nichols and Hines 1993, Diefenbach and Alt 1998).

The model that we described in the first part of this article can easily be extended to accommodate individual and group effects using program MARK. This is illustrated in the mallard duck example where we were able to fit an age- and sex-dependent model as well as allowing birds associated with the banding site to have different reporting rates to other birds. An alternative approach to having the reporting rate differ following each recapture is to have different parameters for birds in their first year following banding. Such a temporary marking-effect model can be easily fitted. One approach is to split the encounter history into 2 parts, 1 for the period when the animal has not yet been recaptured and 1 for the period following first recapture (see Pradel 1993). An alternative approach is to use time-specific, individual covariates. Each animal would have individual covariates for each interval, with 1 indicating an interval immediately following first capture, and 0 indicating otherwise. These individual covariates can then be included in the design matrix to estimate the response to initial capture, and evaluate the importance of this effect.

The concept of using all re-encounter information can be extended to other mark-recapture designs, such as the multi-state model and Pollock's robust design. The multi-state model would be a useful development for the paradise shelduck study because the birds were banded at 3 separate banding sites, and the original intent was to examine movement of birds between these banding sites (Barker 1990). Such a model may also account for the lack of fit indicated by the bootstrap goodness of fit test. Currently, the only software available for doing this does not allow use of the recovery information.

Finally, none of the joint models that have been developed so far include abundance, recruitment, or population change parameters. In principle, the modeling approach adopted by Pradel (1996) for incorporating recruitment parameters in the JS model

(Pradel 1996) can be extended to joint models for live-recapture, dead recoveries, and live-recaptures. In this case, the extra information provided by resightings or recoveries does not provide any direct information on recruitment because recruitment information is provided by captures of unmarked animals. However, the additional information should improve recruitment estimates indirectly through better modeling of the capture and survival processes.

Acknowledgments. M. McDougall, D. McMillan, and B. Williams were key contributors to the paradise shelduck banding study and P. Taylor, S. Smith and I. Buchanan to the mallard banding study. Thanks to I. Ludwichowski and S. Bräger for allowing use of the common goldeneye data and to M. O'Neill for reviewing an early draft of this manuscript. This work was partially funded by the Marsden Fund and the NZ/USA Co-operative Science Programme, both administered by the Royal Society of New Zealand.

LITERATURE CITED

- BARKER, R. J. 1990. Recoveries of Paradise shelduck banded in the Wanganui District. *Notornis* 37:173-181.
- . 1995. Open population mark-recapture models including ancillary sightings. Dissertation, Massey University, New Zealand.
- . 1997. Joint modeling of live-recapture, tag-resight, and tag-recovery data. *Biometrics* 53:666-677.
- BROWNIE, C., D. R. ANDERSON, K. P. BURNHAM, AND D. S. ROBSON. 1978. Statistical inference from band recovery data—a handbook. U.S. Fish and Wildlife Service Resource Publication 131.
- , ———, AND ———. 1985. Statistical inference from band recovery data—a handbook. Second edition. U.S. Fish and Wildlife Service Resource Publication 156.
- , J. E. HINES, J. D. NICHOLS, K. H. POLLOCK, AND J. B. HESTBECK. 1993. Capture-recapture studies for multiple strata including non-Markovian transitions. *Biometrics* 49:1173-1187.
- , AND D. S. ROBSON. 1983. Estimation of time-specific survival rates from tag-resighting samples: a generalization of the Jolly-Seber model. *Biometrics* 39:437-453.
- BUCKLAND, S. T. 1980. A modified analysis of the Jolly-Seber capture-recapture model. *Biometrics* 36:419-435.
- BURNHAM, K. P. 1993. A theory for combined analysis of ring recovery and recapture data. Pages 199-213 in J. D. Lebreton and P. North, editors. *Marked individuals in bird population studies*. Birkhauser Verlag, Basel, Switzerland.
- , AND D. R. ANDERSON. 1998. *Model selection and inference: a practical information theoretic approach*. Springer-Verlag, New York, New York, USA.
- CATCHPOLE, E. A., S. N. FREEMAN, B. J. T. MORGAN, AND M. P. HARRIS. 1998. Integrated recovery/recapture data analysis. *Biometrics* 54:33-46.
- CAUGHLEY, G. 1977. *Analysis of vertebrate populations*. John Wiley & Sons, Chichester, United Kingdom.
- CLOBERT, J. 1995. Capture-recapture and evolutionary ecology: a difficult wedding? *Journal of Applied Statistics* 22:989-1008.

- CORMACK, R. M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51:429–438.
- COX, D. R., AND D. V. HINKLEY. 1974. *Theoretical statistics*. Chapman & Hall, London, United Kingdom.
- DIEFENBACH, D. R., AND G. L. ALT. 1998. Modeling and evaluation of ear tag loss in black bears. *Journal of Wildlife Management* 62:1292–1300.
- JOLLY, G. M. 1965. Explicit estimates from capture–recapture data with both death and immigration–stochastic model. *Biometrika* 52:225–247.
- KENDALL, W. L., J. D. NICHOLS, AND J. E. HINES. 1995. Estimating temporary emigration using capture–recapture with Pollock’s robust design. *Ecology* 78:563–578.
- LEBRETON, J. D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- MARDEKIAN, S. Z., AND L. McDONALD. 1981. Simultaneous analysis of band-recovery and live-recapture data. *Journal of Wildlife Management* 45:484–488.
- NELSON, L. J., D. R. ANDERSON, AND K. H. BURNHAM. 1980. The effect of band loss on estimates of annual survival. *Journal of Field Ornithology* 51:30–38.
- NICHOLS, J. D., AND J. E. HINES. 1993. Survival rate estimation in the presence of tag loss using joint analysis of capture–recapture and resighting data. Pages 229–242 in J. D. Lebreton and P. M. North, editors. *Marked individuals in the study of bird populations*. Birkhauser Verlag, Basel, Switzerland.
- POLLOCK, K. H. 1982. A capture–recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46:757–760.
- PRADEL, R. 1993. Flexibility in survival analysis from recapture data: handling trap-dependence. Pages 29–37 in J. D. Lebreton and P. North, editors. *Marked individuals in bird population studies*. Birkhauser Verlag, Basel, Switzerland.
- . 1996. Utilization of capture–mark–recapture for the study of recruitment and population growth rate. *Biometrics* 52:703–709.
- SEBER, G. A. F. 1965. A note on the multiple-recapture census. *Biometrika* 52:249–259.
- . 1982. *The estimation of animal abundance and related parameters*. Griffin, London, United Kingdom.
- SZYMCZAK, M. R., AND E. A. REXSTAD. 1991. Harvest distribution and survival of a gadwall population. *Journal of Wildlife Management* 55:592–600.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 Supplement:120–138.
- , ———, AND D. R. ANDERSON. 2001. Advanced features of program MARK. Pages 368–377 in R. Field, R. J. Warren, H. Okarma, and P. R. Sievert, editors. *Wildlife, land, and people: priorities for the 21st century*. Proceedings of the Second International Wildlife Management Congress. The Wildlife Society, Bethesda, Maryland, USA.