Ring-Recovery Methods for Historical Ringing Data

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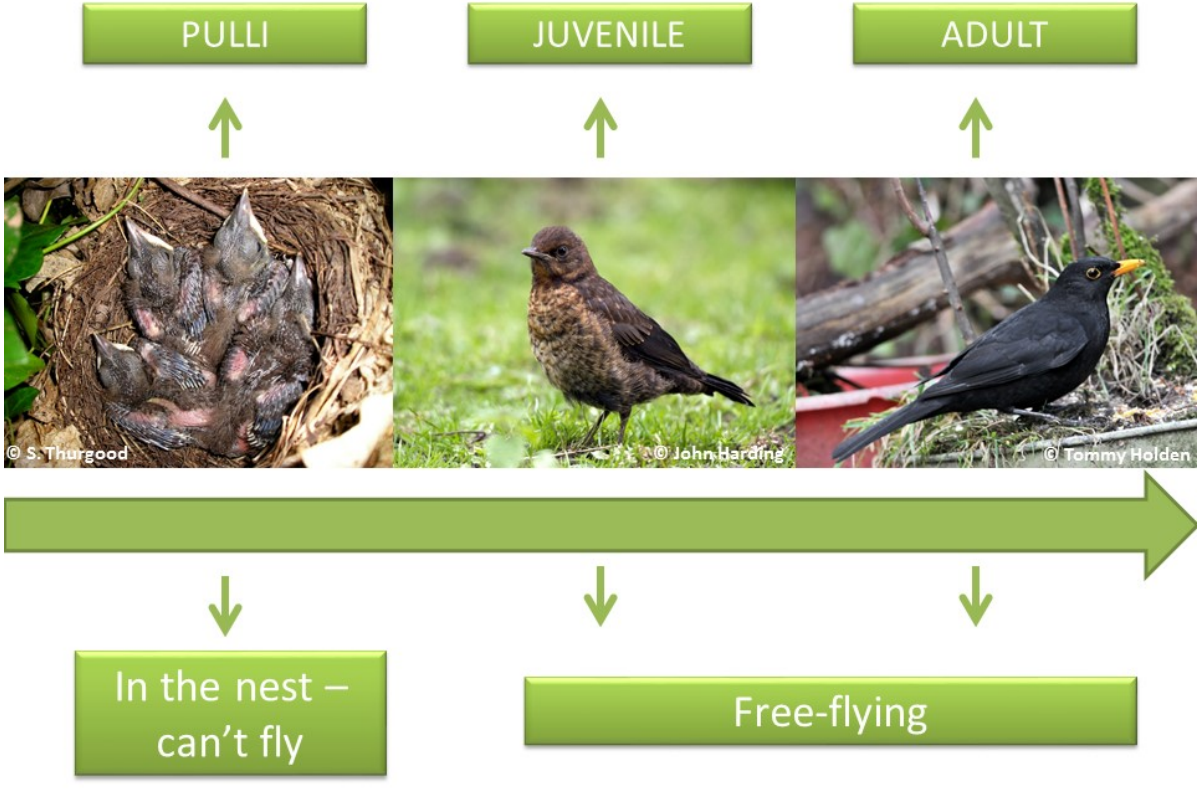
INTRODUCTION

- Ringing schemes in Britain since the beginning of the **20th century**.
- Nearly all records of birds that have been recovered have been computerised.
- Historical ringing totals for the different age classes for some species are only in paper form.

RING-RECOVERY DATA

- Ring-recovery models require data on:
  - The **total number of birds ringed in each age category** (i.e. pulli, juvenile and adult birds),
  - The **total number of recoveries for each age category**.

STANDARD RING-RECOVERY DATA



HISTORICAL RING-RECOVERY DATA

- For some species, like the Sandwich tern, not all historical data has been computerised:
  - **UNKNOWN total number of birds ringed in each age category**
  - **KNOWN total number of recoveries for each age category**
- **Survival** tends to be **affected by age**. While **older birds** are likely to have a **more stable and higher survival rate**, **younger birds** usually have a **more varying and smaller chance of surviving**.

HISTORIC RING-RECOVERY DATA

HISTORIC RING-RECOVERY DATA

- Robinson R. A. (2010) [1] assumes *a priori* proportions of the birds ringed as free-flying are marked as juveniles.
- We propose a model in which this proportion can be estimated as a parameter.
  - This model extends the results of Robinson R. A. (2010),
  - We show that this proportion can be estimated, along with other parameters.

[1] Robinson R. A. (2010). Estimating age-specific survival rates from historical ringing data. *The International Journal of Avian Science*, **152**, 651-663.

DATA


Sandwich Tern *Sterna sandvicensis*
Blackbirds *Turdus merula*
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DATA

Table: Total number of Sandwich Terns ringed and recovered in each age category.

Age at ringing	No. of birds ringed	Percentage of Total birds ringed	No. of birds recovered
Pulli	67008	98.18%	851
Free-flying birds	1244	01.82%	37
Total	68252	100.00%	888

Table: Total number of Blackbirds ringed and recovered in each age category.

Age at ringing	No. of birds ringed	Percentage of Total birds ringed	No. of birds recovered
Pulli	71768	29.58%	2194
Free-flying birds	170858	70.42%	5595
Juvenile	96391	39.73%	3255
Adult	744667	30.69%	2340
Total	242626	100.00%	7789

MODELS

Table: Description of the models used. (The models in bold are the models developed in this paper).

Model name	Data on birds ringed as	Totals known?
Standard	pulli or adults	yes
Standard Combined	free-flying: juveniles and adults	yes
Standard Combined	pulli and free-flying: juveniles and adults	yes
Historic	Free-flying: juveniles and adults	no
Historic Combined	All age-categories: pulli and free-flying	pulli only
Conditional	Free-flying: juveniles and adults	no
Conditional Combined	All age-categories: pulli and free-flying	pulli only

STANDARD MODEL

- Brownie *et al.* (1985)[2], Freeman and Morgan (1992)[3]
- Standard Model:
  - Pulli or adults
- Standard Combined Model:
  - Free-flying: juveniles and adults
  - Pulli and free-flying: juveniles and adults

[2]Brownie, C., Anderson, D. R., Burnham, K. P., and Robson, D. S. (1985). Statistical inference from band recovery data handbook. Resource Publication. No. 156.Washington, DC: United States Department of the Interior, Fish and Wildlife Service.

[3]Freeman S. N. and Morgan B. J. T. (1992). A modelling strategy for recovery data from birds ringed as nestlings. *Biometrics*, **48**: 217-235.

STANDARD MODEL

- n_1 years of ringing and n_2 years of recovery,
- **Known** $T_{i,1}$ and $T_{i,a}$, total number of birds ringed as juveniles and adults in year i,
- **Known**, $N_{i,t,1}$ and $N_{i,t,a}$, number of juvenile, and adult birds that were ringed in year i and recovered dead in year t,

  where $i = 1, \ldots, n_1$, and $t = 1, \ldots, n_2$.

The models depend on the following parameters:

- $\phi_{1,t}$, probability of survival for a juvenile bird at time t;
- $\phi_{a,t}$, probability of survival for an adult bird at time t;
- $\lambda_{1,t}$,recovery probability for a juvenile bird at time t;
- $\lambda_{a,t}$ is the recovery probability for an adult bird at time t.

STANDARD MODEL

The probability that a bird ringed in year i is recovered in year t in the first age class,

$$P_{i,t,1} = \begin{cases} (1-\phi_{1,t})\lambda_{1,t} & \text{if } t = i \\ \phi_{1,i}\left(\prod_{k=i+1}^{t-1}\phi_{a,k}\right)(1-\phi_{a,t})\,\lambda_{a,t} & \text{if } t > i \end{cases}$$

for $i = 1, \ldots, n_1$, $t = i \ldots, n_2$.
The probability that a bird ringed in year i is recovered in year t in the adult age class is denoted by $P_{i,t,a}$ with,

$$P_{i,t,a} = \left(\prod_{k=i}^{t-1}\phi_{a,k}\right)(1-\phi_{a,t})\,\lambda_{a,t}$$

for $i = 1, \ldots, n_1$, $t = i, \ldots, n_2$.

STANDARD MODEL - LIKELIHOOD

Likelihood for standard model for Pulli data,

$$L_S \propto \prod_{i=1}^{n_1} \left\{ \prod_{t=i}^{n_2} P_{i,t,1}^{N_{i,t,1}} \left(1 - \sum_{t=i}^{n_2} P_{i,t,1}\right)^{T_i - \sum_{t=i}^{n_2} N_{i,t,1}} \right\}.$$

If the free-flying data was fully computerised the likelihood for the standard combined model,

$$L_{SC} \propto \left\{ \prod_{i=1}^{n_1} \prod_{t=i}^{n_2} P_{i,t,1}^{N_{i,t,1}} P_{i,t,a}^{N_{i,t,a}} \right\} \times \left\{ \prod_{i=1}^{n_1} \left(1 - \sum_{t=i}^{n_2} P_{i,t,1}\right)^{T_{i,1} - \sum_{t=i}^{n_2} N_{i,t,1}} \times \left(1 - \sum_{t=i}^{n_2} P_{i,t,a}\right)^{T_{i,a} - \sum_{t=i}^{n_2} N_{i,t,a}} \right\}.$$

HISTORIC MODEL

- **Unknown** number of free-flying birds ringed in each age class, we only know T_i, total number of birds ringed in each year i
- **Known**, $N_{i,t,1}$ and $N_{i,t,a}$, number of juvenile, and adult birds that were ringed in year i, and recovered dead in year t
- Historic Model:
  - Free-flying
- Historic Combined Model:
  - Pulli and free-flying

Additional parameter:

- p_t, the proportion of juvenile birds ringed at time t, with $(1 - p_t)$ adult birds ringed.

HISTORIC MODEL

The probability that a bird ringed in the first age class in year i is recovered in year t,

$$Q_{i,t,1} = \begin{cases} p_t(1-\phi_{1,t})\lambda_{1,t} & \text{if } t = i \\ p_t\phi_{1,t}\left(\prod_{k=i+1}^{t-1}\phi_{a,k}\right)(1-\phi_{a,t})\,\lambda_{a,t} & \text{if } t > i \end{cases}$$

for $i = 1, \ldots, n_1$, $t = i, \ldots, n_2$.
The probability that a bird ringed in the adult age class in year i is recovered in year t,

$$Q_{i,t,a} = \quad (1-p_t)\left(\prod_{k=i}^{t-1}\phi_{a,k}\right)(1-\phi_{a,t})\,\lambda_{a,t}$$

for $i = 1, \ldots, n_1$, $t = i, \ldots, n_2$.

HISTORIC MODEL - LIKELIHOOD

The likelihood for the historic model for free flying birds

$$L_H = \left\{ \prod_{i=1}^{n_1} \prod_{t=i}^{n_2} Q_{i,t,1}^{N_{i,t,1}} Q_{i,t,a}^{N_{i,t,a}} \right\} \times \left\{ \prod_{i=1}^{n_1} \left(1 - \sum_{t=i}^{n_2} Q_{i,t,1} + Q_{i,t,a} \right)^{T_i - \sum_{t=i}^{n_2} (N_{i,t,1} + N_{i,t,a})} \right\}.$$

The likelihood for the historic combined model

$$L_{HC} \propto \left\{ \prod_{i=1}^{n_1} \prod_{t=i}^{n_2} Q_{i,t,1}^{N_{i,t,1}} Q_{i,t,a}^{N_{i,t,a}} P_{i,t,p}^{N_{i,t,p}} \right\} \times \left\{ \prod_{i=1}^{n_1} \left(1 - \sum_{t=i}^{n_2} Q_{i,t,1} + Q_{i,t,a} \right)^{T_i - \sum_{t=i}^{n_2} (N_{i,t,1} + N_{i,t,a})} \times \left(1 - \sum_{t=i}^{n_2} P_{i,t,p} \right)^{T_{i,p} - \sum_{t=i}^{n_2} N_{i,t,p}} \right\},$$

where $N_{i,t,p}$ is the number of pulli ringed in year i who were recovered dead in year t and $T_{i,p}$,the total number pulli ringed in year i. The probability that a pulli ringed in year i is recovered in year t is $P_{i,t,p} = P_{i,t,1}$.

CONDITIONAL MODEL

- McCrea *et al.* (2012)[4]
- Alternative to the historic Model, assumes totals unknown
- Conditional Model:
  - Free-flying
- Conditional Combined Model:
  - Pulli and free-flying

The conditional probabilities for birds ringed in year i that are recovered in year t, in both age class are

$$P^C_{i,t,1} = \frac{P_{i,t,1}}{\sum_{t=i}^{n_2} P_{i,t,1}} \text{ and } P^C_{i,t,a} = \frac{P_{i,t,a}}{\sum_{t=i}^{n_2} P_{i,t,a}}.$$

[4]McCrea, R. S., Morgan, B.J.T., Brown D. I. and Robinson R. A. (2012). Conditional modelling of ring-recovery data. *Methods in Ecology and Evolution*, **3**,823-831.

CONDITIONAL MODEL - LIKELIHOOD

The likelihood for the conditional model for the free-flying birds

$$L_C = \prod_{i=1}^{n_1} \prod_{t=i}^{n_2} (P^C_{i,t,1})^{N_{i,t,1}} (P^C_{i,t,a})^{N_{i,t,a}}.$$

The likelihood for the conditional combined model

$$L_{CC} = \prod_{i=1}^{n_1} \prod_{t=i}^{n_2} (P^C_{i,t,1})^{N_{i,t,1}} (P^C_{i,t,a})^{N_{i,t,a}} P_{i,t,p}^{N_{i,t,p}} \times \prod_{i=1}^{n_1} (1 - \sum_{t=i}^{n_2} P_{i,t,p})^{T_{i,p} - \sum_{t=i}^{n_2} N_{i,t,p}}.$$

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FREEMAN-MORGAN MODEL

- Introduce model notation x/y/z:
  - x: first-year-survival probability, ϕ_1
  - y: adult-survival probability, ϕ_a
  - z: recovery probability, λ
- Possible parameter dependencies
  - C: constant
  - CA: constant dependence for the 2 age classes
  - T: time dependence
  - TA: time dependence for the 2 age classes

PARAMETER REDUNDANCY

- Some parameters in a model cannot be estimated.
- Its presence may lead to biased/inaccurate results. separately.
- Causes:
  - Structure of the model
    - symbolic algebra
  - Use of inefficient or insufficient data
    - Simulated data,
    - Blackbird data: we have all the ringing totals,
    - Sandwich tern data: we do not have all the ringing totals.

PARAMETER REDUNDANCY

Model	standard	historic		hist. comb.	conditional	cond. comb.
Data set(s)	Pulli	FF		Pulli + FF	FF	Pulli + FF
Proportion	NA	C	T	C or T	NA	NA
C/C/C/...	0	0	0	0	0	0
C/C/T/...	0	0	0	0	2	0
C/C/CA/...	1	1	0	0	2	1
C/C/TA/...	1	1	2	0	3	1
C/T/C/...	0	0	0	0	0	0
C/T/T/...	0	0	0	0	3	0
C/T/CA/...	1	1	0	0	2	1
C/T/TA/...	2	2	3	1	$n+2$	3
T/C/C/...	0	0	0	0	0	0
T/C/T/...	0	0	0	0	2	0
T/C/CA/...	0	0	0	0	2	0
T/C/TA/...	2	2	3	1	$n+1$	3
T/T/C/...	0	0	0	0	1	0
T/T/T/...	2	1	1	1	$n+1$	2
T/T/CA/...	0	0	0	0	3	0
T/T/TA/...	$n+1$	3	4	2	$2n$	$n+2$

RESULTS - SIMULATION STUDY

Table: Simulation study for 5 years of ringing and recovery of study and for given true parameter values.

parameter	true value	standard model			historic model			historic fixed $p = 0.4$			historic fixed $p = 0.2$		
		av par est	MSE	av se	av par est	MSE	av se	av par est	MSE	av se	av par est	MSE	av se
ϕ_1	0.4	0.40	0.006	0.08	0.40	0.006	0.08	0.40	0.006	0.08	0.47	0.023	0.12
ϕ_a	0.6	0.60	0.004	0.07	0.60	0.004	0.07	0.60	0.004	0.07	0.79	0.053	0.09
λ	0.3	0.30	0.001	0.03	0.30	0.001	0.04	0.30	0.001	0.03	0.57	0.154	0.16
p	0.4				0.40	0.002	0.05						

RESULTS - HISTORIC MODEL

Table: Comparison between the historic ring-recovery and standard combined model selection for Blackbirds.

Historic free-flying totals	Δ AIC	Standard Combined Juveniles + adults totals	Δ AIC
C/C/T/T	0.00	C/C/T	0.00
C/T/T/T	3.68	C/T/T	11.89
C/C/T/C	6.65		
C/T/T/C	18.30		
T/C/T/C	20.30	T/C/T	23.87
T/C/T/T*	22.59		
C/C/C/C	148.56	C/C/C	140.58

Parameter redundant models are marked with '*'.

RESULTS - COMBINED MODEL

Table: Comparison for historic combined and standard combined ring-recovery model selection for Blackbirds

Historic Combined pulli + free flying totals	Δ AIC	Standard Combined pulli + juveniles + adults totals	Δ AIC
C/C/TA/C	0.00	C/C/TA	26.48
T/C/T/C	2.30	T/C/T	38.38
C/C/T/T	2.60	C/C/T	0.00
C/C/TA/T	5.10		
C/C/T/C	5.80		
C/T/T/T	17.70	C/T/T	30.40
C/C/C/C	146.10	C/C/C	148.33

RESULTS - SANDWICH TERNS

Table: Standard ring-recovery model selection for Sandwich Tern 1970-1990.

Model	Δ AIC	parameters	estimable pars.	total pars.
C/T/T	0.00	$\phi_1, \phi_{a,t}, \lambda_t$	40	40
C/C/T	0.66	$\phi_1, \phi_a, \lambda_t$	23	23
C/T/C	4.52	$\phi_1, \phi_{a,t}, \lambda$	22	22
C/C/C	38.16	ϕ_1, ϕ_a, λ	3	3

Table: Historic ring-recovery model selection for Sandwich Terns 1970-1990.

Model	Δ AIC	parameters	estimable pars.	Total pars.
C/C/C/C	0.00	$\phi_1, \phi_a, \lambda, p$	4	4
C/C/T/C*	1.49	$\phi_1, \phi_a, \lambda_j, p$	24	24
C/T/T/C* $n_2 = n_1$	32.22	$\phi_1, \phi_{a,j}, \lambda_j, p$	?	43
T/C/T/C*	37.61	$\phi_{1,j}, \phi_a, \lambda_j, p$	?	44

Table: Historic Combined ring-recovery model selection for Sandwich Terns for 1970-1990.

Model	Δ AIC	parameters	estimable pars.	Total pars.
C/C/T/C	0.00	$\phi_1, \phi_a, \lambda_j, p$	24	24
C/C/C/C	27.67	$\phi_1, \phi_a, \lambda, p$	4	4
T/C/C/C	34.01	$\phi_{1,j}, \phi_a, \lambda, p$	24	24

RESULTS SANDWICH TERNS

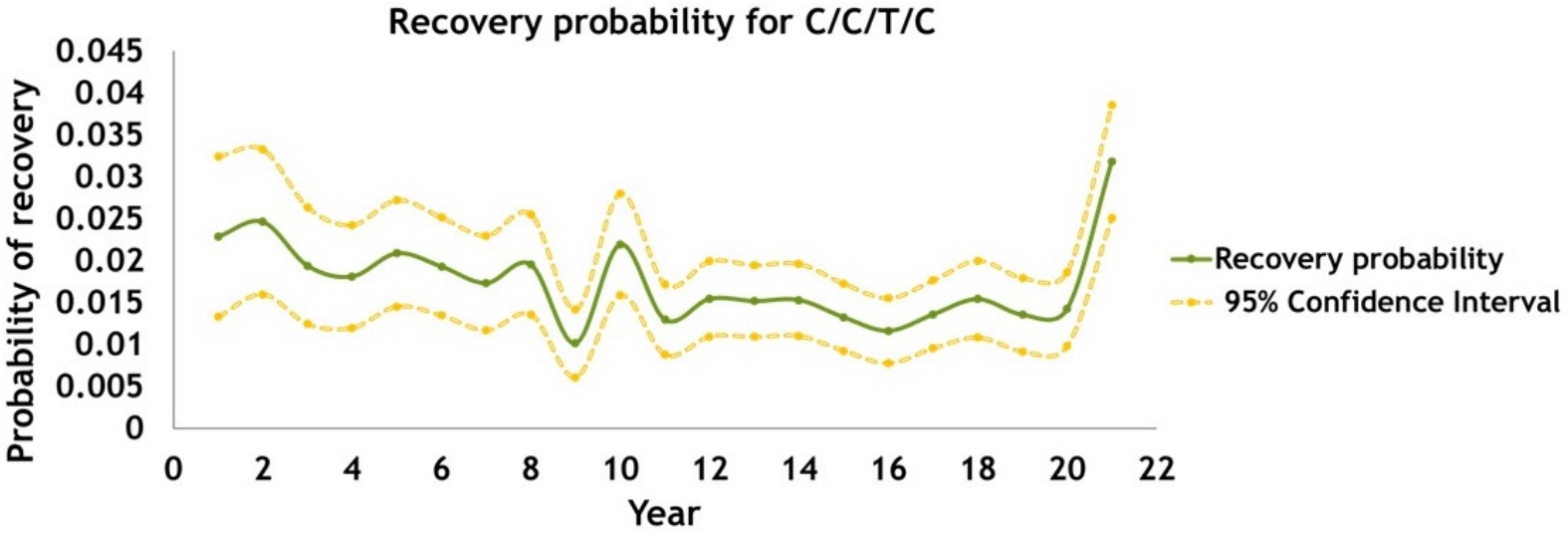

Table: Parameter estimates for C/C/T/C historic combined model.

ϕ_1	ϕ_a	p
0.8697(0.0099)	0.7418(0.0163)	0.3151(0.0757)

SUMMARY

- Using identifiability theory we show that it is possible to extend the adhoc method presented in Robinson (2010), to create a model, where the proportion can be estimated.
- The historic model is an alternative to the conditional model. However, in the conditional model few models can be used due to parameter redundancy.
- The historic model is almost as good as the standard model, but without the need of fully computerised data.
- The model for younger birds is easily extended to additional survival or reporting rates for second and third years if required.
- Potential for extension to fit capture-recapture or capture-recapture-recovery models with uncertainty in age or sex categories.
- R code available to fit all the models described here.