

Multistate measurements of genotype interchange between East Australia and Oceania (IWC breeding sub-stocks E1, E2, E3 and F2) between 1999 and 2004

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ABSTRACT

Humpbacks breeding in east Australia (E1) and Oceania (New Caledonia E2, Tonga E3 and French Polynesia F2) in the South Pacific are thought to be demographically independent, due to significant differentiation of mitochondrial DNA haplotypes between regions, and notable differences in the trend and pattern of recovery across the South Pacific. Matching of fluke photo-identification and microsatellite genotypes collected across the South Pacific has revealed multiple inter-annual movements between breeding grounds. Total documented movements within Oceania are greater than those documented between Oceania and east Australia, which indicates that east Australia may be more isolated from Oceania than the breeding grounds within Oceania are from each other. A strong contrast in population trend between these regions further supports this observation. A large microsatellite genotype dataset of 1,393 individuals (819 males and 574 females) spanning 1999-2004 is available from all South Pacific breeding grounds. We use this to build the first multistate movement model for the South Pacific region and to estimate rates of inter-breeding ground interchange in a framework that accounts for capture probabilities and survival through time. Thirteen inter-annual, inter-strata movements were identified; 10 males and 3 females. The data are too sparse to permit strong inference regarding movement among breeding grounds. However they do suggest that movements between east Australia and New Caledonia (southwestern Pacific) are not significantly different from intra-Oceania movements between New Caledonia and Tonga, indicating that population connectivity levels between east Australia, New Caledonia and Tonga are of similar, low magnitude, despite a pronounced difference in population trend between east Australia and all Oceania regions over the survey period. These results should be taken into consideration when grouping New Caledonia, Tonga and French Polynesia as a single unit for assessment since such an assessment may fail to account for different patterns of recovery and trend within the South Pacific.

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) gather to breed at multiple wintering sites scattered across a vast longitudinal range in the western South Pacific (145°E-120°W), along the Great Barrier Reef of eastern Australia (EA), in the lagoons and seamounts of New Caledonia (NC), and among the islands and atolls of Tonga (TG) and French Polynesia (FP). Fluke photo-identification, microsatellite genotypes and satellite telemetry suggest that whales breeding offshore of east Australia and New Caledonia may visit a common Southern Ocean feeding ground in Antarctic Area V (130-180°E) (Chittleborough 1965; Constantine *et*

al. 2011; Franklin *et al.* In press-a; Gales *et al.* 2009; Steel *et al.* 2008; Steel *et al.* 2011), travelling via New Zealand, Norfolk Island or the east Australian coastline (Dawbin 1956; Dawbin 1964; Franklin *et al.* 2011; Gales *et al.* 2009; Garrigue *et al.* 2010) while additional eastern migratory routes are hypothesized for whales breeding in Tonga and French Polynesia, some of which travel past the Cook Islands (Hauser *et al.* 2010) to and from wintering grounds in Area VI (180°E-100°W) or even the Antarctic Peninsula (Robbins *et al.* 2011; South Pacific Whale Research Consortium 2008). In addition to the multiple migratory routes and vast distance over which these breeding grounds are spread, additional evidence of demographic isolation between breeding grounds is provided by genetic data, which shows significant differentiation between all regions according to F_{ST} metrics (Olavarria *et al.* 2006; Olavarria *et al.* 2007).

The South Pacific Whale Research Consortium has been conducting field surveys of humpbacks in Oceania since 1991. In 1999, the Consortium began a six-year coordinated survey of the four primary island regions of Oceania: New Caledonia (primarily the southern tip of Grand Terre), Tonga (Vava'u), the Cook Islands (Rarotonga) and French Polynesia (Moorea and Rurutu), collecting fluke photo-identifications and genetic biopsies. These have been coordinated with similar surveys off the coast of east Australia (Anderson 2010; Franklin *et al.* In press-b) in order to facilitate a comparison of population connectivity both within Oceania and between Oceania and east Australia. When the Oceania fluke catalogue was matched to east Australia fluke catalogues, only four matches were found among over 710,000 comparisons suggesting extremely low levels of interchange with east Australia (Garrigue *et al.* 2011b). Matches of humpbacks within Oceania suggested relatively higher rates of movement, although movements were still much rarer than resights within individual breeding grounds (Garrigue *et al.* 2011a). This led to the Oceania stock structure hypothesis wherein each breeding ground is considered a sub-stock (E1, E2, E3, F2) but for population assessment purposes the Oceania sub-stocks E2, E3 and F2 have been grouped into one combined unit and E1 was assessed as a separate unit (Jackson *et al.* 2009). A recent combined abundance estimate from Oceania suggested a total of roughly 3,000 whales using E2, E3 and F2 in 2003 (Constantine *et al.* 2012) and found no discernible trend in abundance over the survey period (1999-2005). In contrast a very strong trend in abundance has been documented in E1 over the past 20 years (Noad *et al.* 2011; Noad *et al.* 2008), while an anomalous increase in abundance has also recently been reported for New Caledonia (E2, Garrigue *et al.* 2012).

To date no structured, quantitative assessment of inter-breeding ground interchange has been carried out, although a large synoptic dataset of individuals based on microsatellite genotypes is available, and spans the four breeding grounds of the South Pacific over the period 1999-2004. Here we attempt the first quantitative analysis of breeding ground interchange using these data and explore the potential of multistate analysis to test whether levels of interchange with East Australia and Oceania are lower than levels of interchange within Oceania. Multistate models were originally developed to analyze situations where animals change state in an unpredictable fashion, whether changes in life history stage or geographical migration between regions (Arnason 1972, 1973). In this study we focus on Cormack Jolly Seber models which condition only on events since initial marking. In these models only survival (Φ), capture (p) and movement probabilities (ψ) are calculated, where Φ_i^s represents the probability of an animal alive at time j in stratum s remaining alive at $j+1$ in any stratum, and ψ_j^{st} represents the probability of an animal alive at time j in stratum s moving to stratum t at time $j+1$, conditional on surviving to $j+1$. These multistate models assume that all individuals make their transitions at the same time so this model is appropriate for breeding grounds where movements are expected to occur between breeding seasons rather than within them.

METHODS

Datasets

Microsatellite genotype data from Oceania were collected and analyzed as detailed in Constantine *et al.* (2012) in order to obtain individual, sex specific capture histories over the period 1999 to 2004 with up to 17 genetic loci. For Oceania, all individuals that matched at 8 loci and had 1-3 mismatches were reviewed and re-sequenced if necessary; only individuals which successfully amplified for >10 loci were used (Constantine *et al.* 2012). Similar protocols were applied for east Australia and are detailed in Anderson (2010). We used known-sex genotypes from New Caledonia, Tonga and French Polynesia (males=422, females=264). Data from the Cook Islands were not included as it is very sparse in terms of recaptures, has revealed within-season re-sights with Tonga and French Polynesia, and is thought to be a migratory corridor rather than a breeding ground (Hauser *et al.* 2010). Microsatellite genotype data from east Australia (males=397, females=310) were collected from Byron Bay, Hervey Bay and Ballina over the period 1999-2004 as described in Anderson (2010). Genotypes were compared between the two laboratories in order to ensure standardization of techniques (Anderson *et al.* 2003). Data organization, matching and probability of identity analyses were all conducted using GenAlEx (Peakall & Smouse 2006). Total regional captures are given in Table 1 and recaptures and movements between strata are shown in Table 2. Seven movements between east Australia and Oceania were identified over the study period; six connections with New Caledonia and one with Tonga. Total movements between strata are shown in Figure 1. Regional data from east Australia were collapsed into one stratum (EA), as otherwise recaptures were too sparse.

We used the Program MARK (White & Burnham 1999) multistate model framework, which utilizes a first order Markov process to co-estimate sex-specific and capture probabilities (p), survival (Φ) and movement (ψ) (Arnason 1972, 1973; Schwarz *et al.* 1993). Breeding grounds in east Australia, New Caledonia, Tonga and French Polynesia were used as the core strata over the years 1999-2004. Capture probabilities for Tonga were set to zero in 2004 since no samples were available from that year. Genotype data from French Polynesia and from east Australia and Tonga in 1999 were sparse, so we explored data sensitivity to these factors by constructing a second 1999-2004 dataset where French Polynesia was excluded and captures from Tonga in 1999 were excluded. Support for different models was evaluated using the Akaike Information Criterion (AIC) and likelihood ratio testing. Parameter counting was done to ensure that all models were correctly parameterized.

Goodness of fit testing in the Cormack Jolly Seber (CJS) framework was carried out using U-CARE V2.3.2 (Choquet *et al.* 2005). We tested the goodness-of-fit of the general mark-recapture model over all tests: WBWA, 3G.SR, 3G.Sm, M.ITEC, M.LTEC, along with single- and multi-state tests over all strata. Model over-dispersion was also examined by calculating the median c -hat parameter for the most general, fully identifiable model of each data set. In both cases, estimated c -hat was very close (<0.01) to 1, so this adjustment was not applied to either dataset.

RESULTS

Goodness of fit testing only revealed one significant result: New Caledonia males gave a slightly significant ‘transience’ signal via the 3GSR test in 2001 (4.735, $p=0.03$, Appendix 1). It is notable that when the same Oceania genotype dataset was analyzed without east Australia (Constantine *et al.* 2012), the 3GSR test for transience was significant for males across the whole dataset, and for New Caledonia males in 2001 and 2003.

Capture probabilities p

Capture data became sparser across the strata from west to east (Table 1). The most strongly supported multistrata models for both datasets are shown in Tables 2 and 3. More complex (time and sex varying) models were significantly favoured for the east Australia and New Caledonian strata according to likelihood ratio testing (Table 5) while simple (time invariant) models were favoured for Tonga and French Polynesia. In east Australia and New Caledonia the most strongly supported models allowed capture probabilities to differ by sex according to

an additive model where female capture probabilities were a logit-transformed coefficient of the time-varying male capture probabilities (model s+t: 'sex+time'). Female capture probabilities were uniformly lower than those of males. In Tonga and French Polynesia there was no significant difference in support between models with sex-specific or fully constrained time-invariant capture probabilities (Table 4).

Capture probabilities were very similar (<1% difference) between the 3- and 4-strata models (Table 6) for EA, NC and TG. They varied between 3-16% across the survey period for EA, 4-17% for NC and were roughly 4% for TG and 3.5% for FP.

Survival probabilities Φ

The most strongly supported models all had time and region invariant survival probabilities—there was more support for sex-specific survival models, but in many cases estimated survival for both sexes was singular (i.e. $\Phi=1$, $SE=0$), suggesting that there was insufficient information over the time period to accurately estimate this parameter. Fixing annual survival to 0.96 (from Barlow & Clapham 1997) yielded models with much weaker AIC support (i.e. higher AIC).

Movement probabilities ψ

Movement probability estimates were dependent on a small number of documented movements (Figure 1) so as a consequence a number of different movement hypotheses had very similar AICc support, indicating insufficient data to easily distinguish these models. However some generalities could be deduced from the analysis. The best fitting movement models were all time and sex invariant due to the sparseness of documented movements. Where no movements were detected across the survey period (i.e. between east Australia and French Polynesia, and between New Caledonia and French Polynesia), estimates were effectively zero ($\psi < 10^{-10}$). Fixing ψ to zero between these strata usually yielded identical model results. Bidirectional models (models where movements between each pair of strata were equal) were less well supported than the fully directional models; this was significant for the 3-stratum model but not the 4-stratum model, possibly as the latter data were more sparse (Table 4). Fully directional models were also significantly better fitting to both datasets than a model where one movement rate is imposed over all neighbouring strata (Table 4). For 3- and 4- stratum datasets the best supported models gave one interchange rate into New Caledonia from neighbouring strata (east Australia and Tonga) and a second movement rate out of New Caledonia into neighbouring strata. For the 4-stratum dataset a single interchange rate into Tonga from east Australia, New Caledonia and French Polynesia, and out of Tonga to all strata was also strongly supported (Figure 2). A 2-rate movement model was therefore found to be the best fit to both datasets, with movements between strata where no movements have been observed fixed to zero.

Annual movement probabilities from New Caledonia to east Australia and Tonga were estimated at 6.9% (95% CI 3.7-12.4%) in the 4-stratum model and 7.0% (95% CI 3.7-13.1%) in the 3-stratum model. Movement into New Caledonia from east Australia and Tonga was much lower, at 0.5% (95% CI 0.1-2%) in the 4-stratum model and 0.5% (95% CI 0.7-3.8%) in the 3-stratum model (Table 6). These models were strongly supported over those where bidirectional exchange was equal. It is worth noting that the 95% CI values of these estimates are not overlapping for the former estimate and slightly overlapping for the latter, indicating in the former case a possibly significant difference in the two movement rates.

DISCUSSION

Movements are so sparse between breeding grounds that we view the estimated movement parameters in these models with extreme caution; however from this first effort to model interchange in the South Pacific region we learn the following things:

- (1) The data provide no support for a hypothesis of higher movement rates among Oceania breeding grounds compared to between them and east Australia. All strongly supported models gave a roughly 10x higher rate of interchange from New Caledonia to east Australia than from Tonga to New Caledonia.
- (2) The data do not strongly suggest any gross expansion of individuals from east Australia to the breeding grounds to the east, since so few movements ‘from’ east Australia to New Caledonia have been documented. In contrast, the rate of ‘movement’ from New Caledonia to east Australia may be 10x higher. This may be suggestive of east Australian humpbacks using New Caledonian waters on migration and may be explored in more detail by considering the time and capture location of the samples that underlie these movements. The greatly reduced transience signal in New Caledonian males when east Australia is included as a stratum also indicates that this may be a possibility. Valsecchi *et al.* (2010) proposed that the humpback breeding ground off east Australia may be fed by geographically discrete, sex-segregated migratory streams possibly travelling past New Zealand and Norfolk Island as well as along the Australian coastline. Our data suggest a stronger connection between New Caledonia and east Australia than previously thought, which may be consistent with this hypothesis. While only one of the five documented movements between these strata was by a female, females had lower capture probabilities than males in both regions. Sex specific differences in movement rates were not favoured over sex-aggregated movement models (Tables 3 and 4) but this is likely due more to data sparseness than lack of signal, since total inter-stratum movements were of only 10 males and 3 females.
- (3) Capture probabilities were higher for males than for females in east Australia and New Caledonia. In Tonga and French Polynesia there is no support for differences in capture probabilities between the sexes. The biological rationale for this is unclear as Tonga and New Caledonia have similar sample sizes in terms of individual genotypes, although the no data are available from 2004 for the former. It may instead be caused by differences in biopsy sampling approaches in the different breeding grounds, i.e. avoidance of certain age-sex classes.

Management implications

A number of metrics suggest demographic independence among the breeding grounds of the Southwestern Pacific; differences in trend, genetic differentiation and low rates of inter-ground movement relative to intra-ground movement. However the clustering of Oceania breeding grounds into E2/E3/F2 as a distinct unit from east Australia (E1) is not supported by the current analysis. Instead the data support east Australia as being similarly distinct from New Caledonia (E2) as it is from Tonga (E3) to the east. These data suggest that grouping E1 and E2/E3/F2 into two units for assessment may not be an appropriate approach as levels of demographic independence are similar between east Australia, New Caledonia and Tonga, *i.e.*, east Australia may not be more isolated from the southwest Pacific (New Caledonia and Tonga) than animals within the southwest Pacific are from one another. It is hard to comment regarding the autonomy of French Polynesia from other breeding grounds in this analysis, as captures are particularly sparse from that region and only two movements (to/from Tonga) are included in the 1999-2004 genotype survey. Since this survey many years of additional data have been collected, so future analysis of interchange should be more illuminating in this respect.

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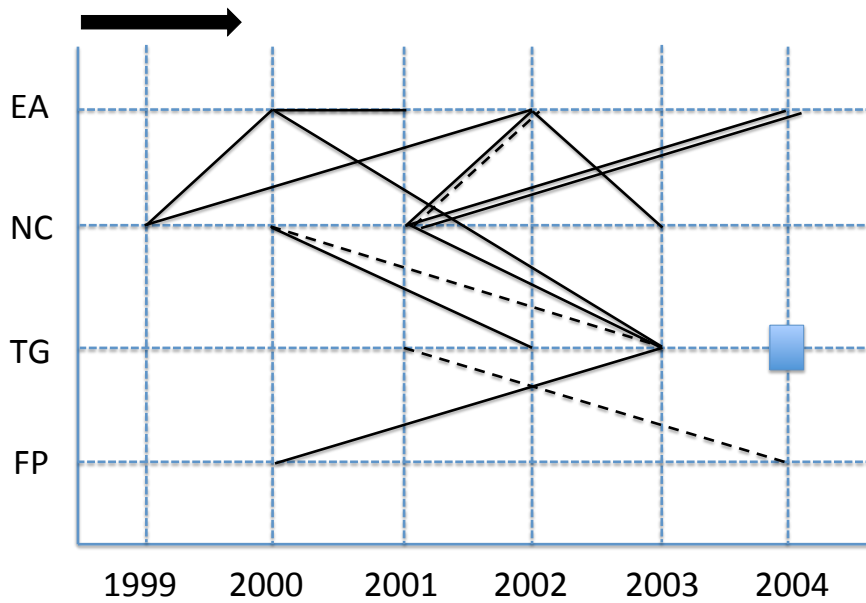


Figure 1. Individual capture histories showing movements from 1999 to 2004 between strata in the South Pacific. Black and dashed lines represent males and female movements respectively. No capture data are available from Tonga in 2004. EA= east Australia, NC=New Caledonia, TG=Tonga, FP=French Polynesia.

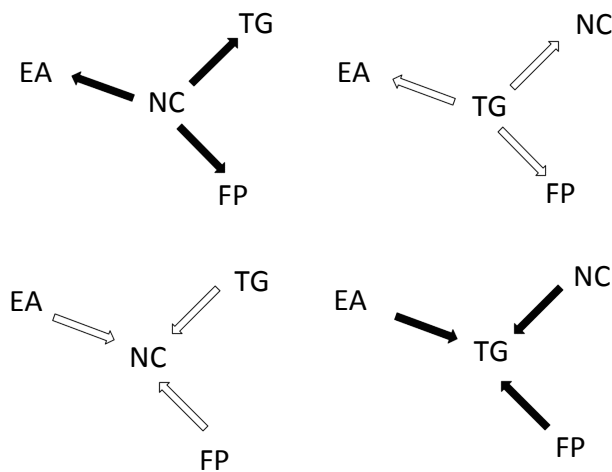


Figure 2. Best fitting interchange model for EA-NC-TG-FP. Black arrow denotes $\Psi=6.9\%$ (95% CI 3.7-12.4%). White arrow denotes $\Psi=0.5\%$, (95% CI 0.1-2.0%).

Table 1. Total captures in each region through time

	Unique IDs	1999	2000	2001	2002	2003	2004
East Australia							
Males	397	2	38	96	128	84	80
Females	310	2	34	91	94	70	46
New Caledonia							
Males	153	15	30	56	15	43	22
Females	107	14	13	33	16	26	22
Tonga							
Males	217	11	34	56	53	76	0
Females	114	9	25	21	23	48	0
French Polynesia							
Males	62	1	8	8	16	12	19
Females	46	2	4	9	7	11	16

Table 2. Within- and between-region genotypic recaptures of males and females respectively from 1999 to 2004

	East Australia	New Caledonia	Tonga	French Polynesia
East Australia	31,23	6,1	1,0	0,0
New Caledonia		20,15	2,1	0,0
Tonga			13, 11	1,1
French Polynesia				2,3

Table 3. Most strongly supported multistrata models for EA-NC-TG-FP dataset (model likelihood range 0.001-1). Model descriptions show probabilities of Capture (p), survival (Φ) and movement (Ψ) by time (t), sex(s), or sex and time invariant (.).

CJS Multistate models (p Φ Ψ)	AICc	Delta AICc	AICc weight	Model likelihood	# P	Deviance
$\Phi(.)$ pEA(t+s) p(NC(t+s) pTG(.) pFP(.) Ψ (NC->EA=NC->TG=EA->TG=FP->TG) Ψ (EA->NC=NC->TG->NC=NC->TG->FP=FP->EA) Ψ (EA<->FP = NC<->FP = 0)	1216.26	0	0.443	1.000	17	193.88
$\Phi(.)$ pEA(t+s) p(NC(t+s) pTG(.) pFP(.) Ψ (NC->EA=NC->TG=EA->TG=FP->TG) Ψ (EA->NC=NC->TG->NC=NC->TG->FP) Ψ (TG->EA) Ψ (EA<->FP = NC<->FP = 0)	1219.60	3.33	0.084	0.190	18	193.10
$\Phi(.)$ pEA(t+s) p(NC(t+s) pTG(.) pFP(.) Ψ (NC->EA=NC->TG = EA->TG =FP->TG) Ψ (EA->NC=NC->TG->NC=NC->TG->FP) Ψ (TG->EA) Ψ (EA<->FP = 0)	1223.72	7.45	0.011	0.024	19	193.10
$\Phi(s)$ pEA(t+s) p(NC(t+s) pTG(.) pFP(.) Ψ (NC->EA=NC->TG =FP->TG) Ψ (EA->NC=NC->TG->NC=NC->TG->FP) Ψ (TG->EA) Ψ (EA<->FP = 0)	1224.22	7.96	0.008	0.019	22	189.47
$\Phi(s)$ pEA(t+s) p(NC(t+s) pTG(.) pFP(.) Ψ (NC->EA=NC->TG=EA->TG=FP->TG) Ψ (EA->NC=NC->TG->NC=NC->TG->FP) Ψ (TG->EA) Ψ (EA<->FP = 0)	1225.75	9.49	0.004	0.009	21	193.08
$\Phi(s)$ pEA(t+s) p(NC(t+s) pTG(.) pFP(.) Ψ (NC->EA=NC->TG) Ψ (EA->NC=NC->TG->NC) Ψ (TG->EA) Ψ (EA->TG) Ψ (TG->FP) Ψ (FP->TG) Ψ (EA<->FP = NC<->FP=0)	1226.66	10.4	0.002	0.006	24	187.77
$\Phi(s)$ pEA(t+s) p(NC(t+s) pTG(.) pFP(.) Ψ (TG->FP=FP->NC) Ψ (NC->TG=FP->TG) Ψ (EA->NC) Ψ (EA->TG) Ψ (NC->EA) Ψ (TG->EA) Ψ (EA<->FP = NC<->FP=0)	1227.78	11.52	0.001	0.003	24	188.89
$\Phi(s)$ pEA(t+s) p(NC(t+s) pTG(.) pFP(.) Ψ (NC->EA=NC->TG) Ψ (EA->NC) Ψ (TG->NC) Ψ (TG->EA) Ψ (EA->TG) Ψ (TG->FP) Ψ (FP->TG) Ψ (EA<->FP = NC<->FP=0)	1228.11	11.85	0.001	0.003	25	187.15
$\Phi(.)$ pEA(t+s) p(NC(t+s) pTG(.) pFP(.) Ψ (NC->EA=NC->TG=EA->NC=NC->TG->NC=NC->TG->EA=EA->TG=NC->FP=FP->TG) Ψ (EA<->FP = NC<->FP=0)	1229.35	13.08	0.001	0.001	15	209.01
$\Phi(s)$ pEA(t+s) p(NC(t+s) pTG(.) pFP(.) Ψ (NC->EA) Ψ (NC->TG) Ψ (EA->NC) Ψ (TG->NC) Ψ (TG->EA) Ψ (EA->TG) Ψ (TG->FP) Ψ (FP->TG) Ψ	1229.80	13.54	0.001	0.001	26	186.76

CJS Multistate models (p Φ Ψ)	AICc	Delta AICc	AICc weight	Model likelihood	# P	Deviance
(EA<->FP = NC<->FP=0) Φ(s) pEA(t+s) p(NC(t+s) pTG(t+s) pFP(.) Ψ(NC->EA) Ψ (NC->TG) Ψ(EA->NC) Ψ (TG->NC) Ψ(TG->EA) Ψ(EA->TG) Ψ(TG->FP) Ψ(FP->TG) Ψ (EA<->FP = NC<->FP=0)	1231.51	15.25	0.000	0.001	30	180.11
Φ(s) pEA(t+s) p(NC(t+s) pTG(s) pFP(s) Ψ(NC->EA) Ψ (NC->TG) Ψ(EA->NC) Ψ (TG->NC) Ψ(TG->EA) Ψ(EA->TG) Ψ(TG->FP) Ψ(FP->TG) Ψ (EA<->FP = NC<->FP=0)	1231.90	15.64	0.000	0.000	28	184.68

Table 4. Most strongly supported multistrata models for EA-NC-TG dataset (model likelihood range 0.001-1). Model descriptions show probabilities of Capture (p), survival (Φ) and movement (Ψ) by time (t), sex(s), or sex and time invariant (.).

CJS Multistate models (p Φ Ψ)	AICc	Delta AICc	AICc weight	Model likelihood	# P	Deviance
$\Phi(.)$ pEA(t+s) pNC(t+s) pTG(.) $\Psi(\text{EA} \rightarrow \text{NC})(.) = (\text{TG} \rightarrow \text{NC})(.)$ $\Psi(\text{EA} \rightarrow \text{TG})(.) = (\text{NC} \rightarrow \text{EA})(.) = (\text{NC} \rightarrow \text{TG})(.)$ $\Psi(\text{TG} \rightarrow \text{EA})(.) = (\text{TG} \rightarrow \text{NC})(.) = 0$	1095.60	0	0.330	1.000	15	146.00
$\Phi(.)$ pEA(t+s) pNC(t+s) pTG(.) $\Psi(\text{EA} \rightarrow \text{NC})(.) = (\text{TG} \rightarrow \text{NC})(.)$, $\Psi(\text{EA} \rightarrow \text{TG})(.)$ $\Psi(\text{NC} \rightarrow \text{EA})(.) = (\text{NC} \rightarrow \text{TG})(.)$, $\Psi(\text{TG} \rightarrow \text{EA})(.) = 0$	1095.80	0.2	0.299	0.907	16	144.15
$\Phi(.)$ pEA(t+s) pNC(t+s)pTG(s) $\Psi(\text{EA} \rightarrow \text{NC})(.) = (\text{TG} \rightarrow \text{NC})(.)$, $\Psi(\text{EA} \rightarrow \text{TG})(.)$ $\Psi(\text{NC} \rightarrow \text{EA})(.) = (\text{NC} \rightarrow \text{TG})(.)$, $\Psi(\text{TG} \rightarrow \text{EA})(.) = 0$	1097.72	2.12	0.114	0.347	17	144.01
$\Phi(s)$ pEA(t+s) pNC(t+s)pTG(.) $\Psi(\text{EA} \rightarrow \text{NC})(.)$ $\Psi(\text{EA} \rightarrow \text{TG})(.) = (\text{NC} \rightarrow \text{EA})(.) = (\text{NC} \rightarrow \text{TG})(.)$ $\Psi(\text{TG} \rightarrow \text{EA})(.) = (\text{TG} \rightarrow \text{NC})(.) = 0$	1099.71	4.11	0.042	0.128	17	146.00
$\Phi(s)$ pEA(t+s) pNC(t+s)pTG(.) $\Psi(\text{EA} \rightarrow \text{NC})(.) = (\text{TG} \rightarrow \text{NC})(.)$, $\Psi(\text{EA} \rightarrow \text{TG})(.)$ $\Psi(\text{NC} \rightarrow \text{EA})(.) = \Psi(\text{NC} \rightarrow \text{TG})(.)$, $\Psi(\text{TG} \rightarrow \text{EA})(.) = 0$	1099.91	4.31	0.038	0.116	18	144.14
$\Phi(s)$ pEA(t+s) pNC(t+s)pTG(.) $\Psi(\text{EA} \rightarrow \text{NC})(.) = (\text{TG} \rightarrow \text{NC})(.)$, $\Psi(\text{EA} \rightarrow \text{TG})(.) = \Psi(\text{NC} \rightarrow \text{EA})(.) = \Psi(\text{NC} \rightarrow \text{TG})(.)$, $\Psi(\text{TG} \rightarrow \text{EA})(.) = 0$	1100.70	5.09	0.026	0.078	17	146.99
$\Phi(s)$ pEA(t+s) pNC(t+s)pTG(.) $\Psi(\text{EA} \rightarrow \text{NC})(.) = (\text{TG} \rightarrow \text{NC})(.)$, $\Psi(\text{EA} \rightarrow \text{TG})(.) = (\text{NC} \rightarrow \text{EA})(.) = \Psi(\text{NC} \rightarrow \text{TG})(.) = (\text{TG} \rightarrow \text{EA})(.) = 0$	1100.70	5.09	0.026	0.078	17	146.99
$\Phi(s)$ pEA(t+s) pNC(t+s) pTG(s) $\Psi(\text{EA} \rightarrow \text{NC})(.)$ $\Psi(\text{EA} \rightarrow \text{TG})(.)$ $\Psi(\text{NC} \rightarrow \text{EA})(.)$ $\Psi(\text{NC} \rightarrow \text{TG})(.)$ $\Psi(\text{TG} \rightarrow \text{EA})(.) = (\text{TG} \rightarrow \text{NC})(.) = 0$	1100.80	5.2	0.025	0.074	19	142.97
$\Phi(s)$ pEA(t+s) pNC(t+s) pTG(s) $\Psi(\text{EA} \rightarrow \text{NC})(.)$ $\Psi(\text{EA} \rightarrow \text{TG})(.)$ $\Psi(\text{NC} \rightarrow \text{EA})(.) = (\text{NC} \rightarrow \text{TG})(.)$ $\Psi(\text{TG} \rightarrow \text{EA})(.) = 0$ $\Psi(\text{TG} \rightarrow \text{NC})(.)$	1100.92	5.32	0.023	0.070	19	143.09
$\Phi(s)$ pEA(t+s) pNC(t+s) pTG(.) $\Psi(\text{EA} \rightarrow \text{NC})(.)$ $\Psi(\text{EA} \rightarrow \text{TG})(.)$ $\Psi(\text{NC} \rightarrow \text{EA})(.)$ $\Psi(\text{NC} \rightarrow \text{TG})(.)$ $\Psi(\text{TG} \rightarrow \text{EA})(.)$ $\Psi(\text{TG} \rightarrow \text{NC})(.) = (\text{TG} \rightarrow \text{EA})(.) = 0$	1100.93	5.33	0.023	0.070	19	143.10
$\Phi(.)$ pEA(t+s) pNC(t+s) pTG(.) $\Psi(\text{EA} \rightarrow \text{NC})(.)$ $\Psi(\text{EA} \rightarrow \text{TG})(.)$ $\Psi(\text{NC} \rightarrow \text{EA})(.)$ $\Psi(\text{NC} \rightarrow \text{TG})(.)$ $\Psi(\text{TG} \rightarrow \text{NC})(.)$ $\Psi(\text{TG} \rightarrow \text{EA})(.) = 0$	1100.94	5.34	0.023	0.069	19	143.11
$\Phi(.)$ pEA(t+s) pNC(s) pTG(.) $\Psi(\text{EA} \rightarrow \text{NC})(.) = (\text{TG} \rightarrow \text{NC})(.)$, $\Psi(\text{EA} \rightarrow \text{TG})(.)$ $\Psi(\text{NC} \rightarrow \text{EA})(.) = (\text{NC} \rightarrow \text{TG})(.)$, $\Psi(\text{TG} \rightarrow \text{EA})(.) = (\text{TG} \rightarrow \text{NC})(.) = 0$	1101.58	5.98	0.017	0.050	12	158.12
$\Phi(s)$ pEA(t+s) pNC(t+s) pTG(.) $\Psi(\text{EA} \rightarrow \text{NC})(.)$ $\Psi(\text{EA} \rightarrow \text{TG})(.)$ $\Psi(\text{NC} \rightarrow \text{EA})(.)$ $\Psi(\text{NC} \rightarrow \text{TG})(.)$ $\Psi(\text{TG} \rightarrow \text{NC})(.)$ $\Psi(\text{TG} \rightarrow \text{EA})(.) = 0$	1102.99	7.39	0.008	0.025	20	143.10
$\Phi(s)$ pEA(t+s) pNC(t+s) pTG(.) $\Psi(\text{EA} \rightarrow \text{NC})(.)$ $\Psi(\text{EA} \rightarrow \text{TG})(.)$ $\Psi(\text{NC} \rightarrow \text{EA})(.)$ $\Psi(\text{NC} \rightarrow \text{TG})(.)$ $\Psi(\text{TG} \rightarrow \text{EA})(.)$ $\Psi(\text{TG} \rightarrow \text{NC})(.)$ }	1105.07	9.47	0.003	0.009	21	143.11

CJS Multistate models (p Φ Ψ)	AICc	Delta AICc	AICc weight	Model likelihood	# P	Deviance
$\Phi(s)$ pEA(t+s) pNC(t+s) pTG(.) Ψ (EA->NC)(.) Ψ (EA->TG)(.) Ψ (NC->EA)(.) Ψ (NC->TG)(.) Ψ (TG->NC)(.) Ψ (TG->EA)(.)	1105.07	9.47	0.003	0.009	21	143.11
$\Phi(s)$ pEA(t+s) pNC(t+s) pTG(s) Ψ (EA->NC)(.) Ψ (EA->TG)(.) Ψ (NC->EA)(.) Ψ (NC->TG)(.) Ψ (TG->EA)(.) Ψ (TG->NC)(.)	1107.01	11.41	0.001	0.003	22	142.97
$\Phi(s)$ pEA(t+s) pNC(s) pTG(.) Ψ (EA->NC)(.) Ψ (EA->TG)(.) Ψ (NC->EA)(.) Ψ (NC->TG)(.) Ψ (TG->EA)(.) Ψ (TG->NC)(.)	1110.57	14.97	0.000	0.001	17	156.86
$\Phi(.)$ pEA(t+s) pNC(t+s) pTG(t+s) Ψ (EA->NC)(s) Ψ (EA->TG)(s) Ψ (NC->EA)(s) Ψ (NC->TG)(s) Ψ (TG->EA)(s) Ψ (TG->NC)(s)	1112.95	17.35	0.000	0.000	28	136.40
$\Phi(s)$ pEA(t+s) pNC(t+s) pTG(t+s) Ψ (EA->NC)(s) Ψ (EA->TG)(s) Ψ (NC->EA)(s) Ψ (NC->TG)(s) Ψ (TG->EA)(s) Ψ (TG->NC)(s)	1113.23	17.63	0.000	0.000	29	134.58
$\Phi(s)$ pEA(s) pNC(t+s) pTG(.) Ψ (EA->NC)(.) Ψ (EA->TG)(.) Ψ (NC->EA)(.) Ψ (NC->TG)(.) Ψ (TG->EA)(.) Ψ (TG->NC)(.)	1113.48	17.88	0.000	0.000	17	159.77

Table 5. Likelihood ratio testing of multistate models. Significant χ^2 values are given in bold.

Model comparison	EA-NC-TG χ^2	EA-NC-TG-FP χ^2
Φ (sex) vs Φ (.)	0.01	0.03
Best Ψ versus fully directional	1.049	
Best Ψ versus all neighbouring Ψ equal	101.40	15.13
Bidirectional versus fully directional model	95.12	6.96
TG (.) vs TG sex	0.13	2.04
FP (.) vs FP sex		1.38
EA(t+sex) vs EA(sex)	79.6	
NC(t+sex) vs NC(sex)	14.0	

Table 6. Multistrata parameter estimates from the best fitting models of the 4 and 3-stratum datasets.

Parameters	4-strata				3-strata			
	Estimate	Standard error	Lower 95%	Upper 95%	Estimate	Standard error	Lower 95%	Upper 95%
Φ (males)	1	0	-	-	1	0.012	0	1
Φ (females)	1	0	-	-	1	0.003	0	1
p(2000) EA males	0.1601	0.1513	0.0206	0.6338	0.1617	0.1528	0.0207	0.6373
p(2001) EA males	0.1084	0.0382	0.0531	0.2087	0.1092	0.0385	0.0535	0.2102
p(2002) EA males	0.0872	0.0206	0.0543	0.1369	0.0879	0.0208	0.0548	0.1382
p(2003) EA males	0.0410	0.0108	0.0244	0.0681	0.0415	0.0109	0.0247	0.0689
p(2004) EA males	0.0311	0.0082	0.0185	0.0518	0.0308	0.0081	0.0183	0.0514
p(2000) EA females	0.1492	0.1438	0.0187	0.6175	0.1505	0.1450	0.0188	0.6207
p(2001) EA females	0.1006	0.0365	0.0483	0.1977	0.1012	0.0367	0.0486	0.1989
p(2002) EA females	0.0808	0.0201	0.0491	0.1300	0.0814	0.0203	0.0495	0.1310
p(2003) EA females	0.0379	0.0106	0.0217	0.0651	0.0382	0.0107	0.0219	0.0658
p(2004) EA females	0.0287	0.0081	0.0165	0.0495	0.0284	0.0080	0.0163	0.0490
p(2000) NC males	0.1335	0.0744	0.0419	0.3520	0.1349	0.0752	0.0423	0.3553
p(2001) NC males	0.1710	0.0562	0.0867	0.3097	0.1734	0.0571	0.0877	0.3140
p(2002) NC males	0.0458	0.0210	0.0184	0.1094	0.0464	0.0213	0.0186	0.1110
p(2003) NC males	0.1603	0.0420	0.0939	0.2601	0.1634	0.0432	0.0951	0.2663
p(2004) NC males	0.0610	0.0206	0.0311	0.1162	0.0655	0.0227	0.0328	0.1267
p(2000) NC females	0.1100	0.0635	0.0335	0.3059	0.1111	0.0642	0.0338	0.3087
p(2001) NC females	0.1420	0.0527	0.0662	0.2785	0.1439	0.0535	0.0670	0.2824
p(2002) NC females	0.0371	0.0183	0.0139	0.0953	0.0375	0.0186	0.0140	0.0966
p(2003) NC females	0.1327	0.0401	0.0717	0.2326	0.1353	0.0413	0.0727	0.2381
p(2004) NC females	0.0495	0.0187	0.0234	0.1019	0.0532	0.0205	0.0247	0.1108
p(.) TG	0.0499	0.0096	0.0341	0.0725	0.0434	0.0095	0.0281	0.0663
p(.) FP	0.0358	0.0145	0.0160	0.0781	NA	NA	NA	NA
Ψ (EA->NC)	0.0049	0.0035	0.0012	0.0198	0.0052	0.0053	0.0071	0.0377
Ψ (EA->TG)	0.0686	0.0214	0.0368	0.1243	0.0704	0.0229	0.0368	0.1308
Ψ (EA->FP)	0.0000	0.0000	0.0000	0.0000	NA	NA	NA	NA
Ψ (NC->EA)	0.0686	0.0214	0.0368	0.1243	0.0704	0.0229	0.0368	0.1308

Parameters	Estimate	Standard error	4-strata		Estimate	Standard error	3-strata	
			Lower 95%	Upper 95%			Lower 95%	Upper 95%
Ψ (NC->TG)	0.0686	0.0214	0.0368	0.1243	0.0704	0.0229	0.0368	0.1308
Ψ (NC<->FP)	0	0	0	0	NA	NA	NA	NA
Ψ (TG->EA)	0.0049	0.0035	0.0012	0.0198	0	0	0	0
Ψ (TG->NC)	0.0049	0.0035	0.0012	0.0198	0	0	0	0
Ψ (TG->FP)	0.0049	0.0035	0.0012	0.0198	NA	NA	NA	NA
Ψ (FP->EA)	0	0	0	0	NA	NA	NA	NA
Ψ (FP->NC)	0	0	0	0	NA	NA	NA	NA
Ψ (FP->TG)	0.0686	0.0214	0.0368	0.1243	NA	NA	NA	NA

APPENDIX

Table 1 Goodness of fit multistate tests. No values were significant except where indicated.

Tests		1999-2004
WBWA	Males	0
	Females	0
3GSR (NC)	Males	10.305
	Males 2001	4.735 (p<0.05)
3G.Sm	Females	6.84
	Males	0
M.ITEC χ^2	Females	0.559
	Males	2.829
g2	Females	1.322
	Males	3.344
M.LTEC	Females	1.702
	Males	0.876
GLOBAL 3G	Females	1.001
	Males	1.106
GLOBAL M	Females	1.048
	Males	10.305
GLOBAL JMV	Females	7.4
	Males	3.705
	Females	2.323
	Males	14.01
	Females	9.723