

# Estimation of survival rates for wader populations: a review of mark-recapture methods

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Wader life-history traits are comprised of low fecundity, delayed maturity and high annual survival. Robust estimates of annual survival are essential for effective conservation because population growth rates of long-lived vertebrates are often sensitive to variation in survivorship. Estimation of survival rates from individually marked waders requires one of three types of data: live encounters, dead recoveries or known-fate information from radio-telemetry. Unfortunately, the available methods for estimation of survival rates vary greatly in their assumptions and utility. Maximum longevity, age-ratios and life-table methods require assumptions that are unlikely to be met in field studies. Return rates have been widely reported for waders but can be difficult to interpret because they are comprised of four independent probabilities: true survival ( $S$ ), site fidelity ( $F$ ), site propensity ( $\gamma^*$ ) and detection ( $p^*$ ). Mark-recapture methods based on live encounter data improve on return rates by estimating apparent survival ( $\phi = S \times F$ ), corrected for the probability of capture ( $p = \gamma^* \times p^*$ ). Fifteen studies have used mark-recapture methods to estimate  $\phi$  and  $p$  for wader populations. Most studies have found that  $\hat{p} < 1$  (95.8%, 23 of 24 estimates), with variation in  $\hat{p}$  often due to sex, year and age-class. A majority of available estimates of apparent survival are based on time-dependent models (63.2%, 12 of 19 estimates). The remaining survival analyses (36.8%, 7 of 19) used models that separated apparent survival in the interval after banding ( $\phi^1$ ) from subsequent intervals ( $\phi^2$ ). These “age”-structured models control for birds captured on only one occasion and yielded better estimates of survival than time-dependent models. Recovery models have been rarely applied to waders, probably because the proportion of ringed birds that are recovered dead is low for nonharvested species ( $< 0.02$ ). Radio-telemetry can yield accurate estimates of daily and seasonal survival but may have limited value for estimating annual survival because radio battery life is short compared to the average life span of waders. New mark-recapture methods, including the multistate, robust design, temporal symmetry, and joint models, have great potential for estimation of demographic rates but have not yet been applied to waders. I discuss potential applications of these statistical models to investigations of wader demography and conclude with specific recommendations for future studies.

## INTRODUCTION

Long-term monitoring programs have revealed troubling population declines among migratory waders in Europe (Tucker & Heath 1994, Hagemeyer & Blair 1997), North America (Howe *et al.* 1989, Morrison *et al.* 2001) and south-east Asia (Rose & Scott 1997). At least 21% of the world's waders (32 of 155 species) are listed as species of conservation concern by Birdlife International (Piersma *et al.* 1997). Conservation efforts for many waders would be aided by a better understanding of their demography. For example, population viability analysis (PVA) is a tool that is frequently used to make conservation decisions for wildlife populations (Beissinger & McCullough 2002), but has been applied to only a few waders (Hill & Carter 1991, Hitchcock & Gratto-Trevor 1997, Larson *et al.* 2002). The simplest PVA models require four types of demographic data: the number of age or stage-classes with unique vital rates, age at first breeding and the mean fecundity and survivorship for each class (Beissinger & Westphal 1998). Most reviews of wader demography stress low reproductive rates (clutch size  $\leq 4$  eggs, high nest failure, 1 brood per year), delayed age of first

breeding and relatively high adult survival (0.7 to 0.9, Evans & Pienkowski 1984, Myers *et al.* 1987, Piersma & Baker 2000). To date, however, relatively little attention has been paid to quantitative methods used to estimate demographic rates for waders.

In this article, I discuss challenges in the estimation of survival and focus on this vital rate for three main reasons. First, survival is a difficult rate to measure under field conditions because the timing and causes of mortality are usually unknown for wild birds. Estimates of seasonal productivity are easier to obtain because the components of reproductive effort can be measured by monitoring nests and broods. Second, estimation of survival rates is a key component of Integrated Population Monitoring, including programs operated by the British Trust for Ornithology (Baillie *et al.* 1999). Last, demographic analyses of waders (Hitchcock & Gratto-Trevor 1997, Larson *et al.* 2002) and other long-lived vertebrates (Brault & Caswell 1993, Doak *et al.* 1994, Crooks *et al.* 1998) often report that survival of adults has a high elasticity value. High elasticity values imply that adult survival should have the greatest potential effect on rates of population change, although low variance in survival



or logistical constraints may favour conservation actions that target other vital rates (Beissinger & McCullough 2002).

The objectives of this article are four-fold: 1) to review the methods that have been used to estimate annual survival rates of waders in the past, 2) to highlight gaps in our current knowledge of survival rates and wader demography, 3) to discuss potential applications of new mark-recapture statistics to the study of wader populations, and 4) to offer specific recommendations for future research.

## ESTIMATION OF ANNUAL SURVIVAL IN WADERS

### Maximum longevity

Records of maximum longevity are frequently reported as evidence of long life in waders (Miller & Reid 1987, Miller & McNeil 1988, Marks 1992, Gratto-Trevor & Vacek 2001, Johnson *et al.* 2001), and the reciprocal of longevity has been used as an index of annual survival (Yom-Tov *et al.* 1992). Longevity records are of interest as a curiosity but should not be used as an index of annual survival because they are a complex function of sample size, ringing effort and senescence, with the net result that they may be a poor predictor of annual survival rates (Kremetz *et al.* 1989). For example, the apparent survival rate of adult European Starlings *Sturnis vulgaris* is moderate and typical of most terrestrial songbirds ( $\hat{S} = 0.649$ , Baillie & McCulloch 1993). However, more than 2 million starlings have been ringed in Europe and the longevity record of this species (20 years, Ehrlich *et al.* 1988) exceeds current longevity records for 33 of 35 North American waders (Klimkiewicz 2002).

### Life-table methods

If a population has a stable age distribution appropriate to a stationary population size, and yearlings and adults are captured in proportion to their abundance in the population, then annual adult survival can be estimated by:

$$\hat{S} = \frac{A}{(Y + A)}$$

where Y = the number of yearling birds in the sample and A is the number of older individuals (Ricklefs 1997). This estimate has little utility for most field studies of waders because it will be biased if population size is fluctuating, if aging criteria are unreliable or if sampling is biased with respect to age. Sampling with respect to age would be biased at breeding sites if yearlings are less likely to migrate north and at wintering sites if differential migration occurs among different age-classes.

If life table data are available for a wader population, age-specific survival rates ( $p_x$ ) can be calculated as:

$$p_x = \frac{l_{x+1}}{l_x}$$

where  $l_x$  is the number of individuals surviving  $x$  years after hatching. Like age ratios, life table methods assume no annual variation in survival and that the population is at a stable age distribution and stationary, although adjustments can be made if the rate of population change is known. Life tables can be constructed with several different types of data

(Williams *et al.* 2002). Horizontal life tables can be constructed by gathering age-specific data by following one (or more) cohorts through time. Using this approach, Holland & Yalden (1991) estimated annual survival rates to be 0.709 for Common Sandpipers *Actitis hypoleucos*. Vertical life tables can be developed if the standing age distribution of a population is known. Dowding & Kennedy (1993) present age distributions for the endangered Shore Plover *Charadrius novaeseelandiae* of New Zealand. Life table analyses of these data yield annual survival rates of 0.755 (B.K. Sandercock, unpubl. analyses). In general, life-table methods have limited practical value because they require data that are rarely available for wader populations (but see Goss-Custard *et al.* 1982). The examples above are exceptions because they were small populations that could be intensively monitored.

### Return rates based on live encounter data

Most estimates of annual survival for waders are based on return rates, the proportion of marked individuals that are recaptured either in the following or some future year (reviews: Evans & Pienkowski 1984, Oring & Lank 1984). Annual return rates in consecutive years can be challenging to interpret because they are the product of four independent probabilities.

- i) true survival ( $S$ ): the probability that a bird survives between two sampling periods.
- ii) site fidelity ( $F$ ): the probability that a bird returns to the same sampling area and does not permanently emigrate, if it survives.
- iii) site propensity ( $\gamma^*$ ): the probability that a bird returns to the same sampling area the next year without skipping a year, if it survives and returns to the same area. Temporary emigration ( $\gamma = 1 - \gamma^*$ ) is the probability that a bird remains part of the "superpopulation" but is unavailable for capture in a particular year.
- iv) detection rates ( $p^*$ ): the probability that an observer detects the bird, if it survives, returns to the same area the next year and is available for capture.

As the product of these four probabilities, return rates are a minimum estimate of true survival. If return rates are high ( $rr > 0.85$ ), then true survival rates must be higher still. High return rates are fairly common among large-bodied waders (e.g.,  $rr = 0.88$ , Black Turnstone *Arenaria melanocephala*, Handel & Gill 2000,  $rr = 0.89$ , Whimbrel *Numenius phaeopus*, Grant 1991,  $rr = 0.89$ , Eurasian Oystercatcher *Haematopus ostralegus*, Durell *et al.* 2000,  $rr = 0.92$ , Bristle-thighed Curlew *Numenius tahitiensis*, Marks & Redmond 1996,  $rr = 0.95$ , Black Oystercatcher *H. bachmani*, Hazlitt & Butler 2001). Difficulties arise in the interpretation of moderate return rates (0.3 to 0.7). Return rates of adult waders often fall within this range (e.g., 8 of 15 species, Oring & Lank 1984) and return rates of waders ringed as hatchlings are often lower ( $< 0.3$ , Oring & Lank 1984, Thompson *et al.* 1994, Sandercock & Gratto-Trevor 1997). Because return rates are the product of multiple probabilities, variation in return rates either among or within species could be due to differences in true survival or may reflect variation in site fidelity, site propensity or detection rates. Return rates are a highly biased estimator of true survival if values of the latter three probabilities are low ( $< 0.8$ , Martin *et al.* 1995).



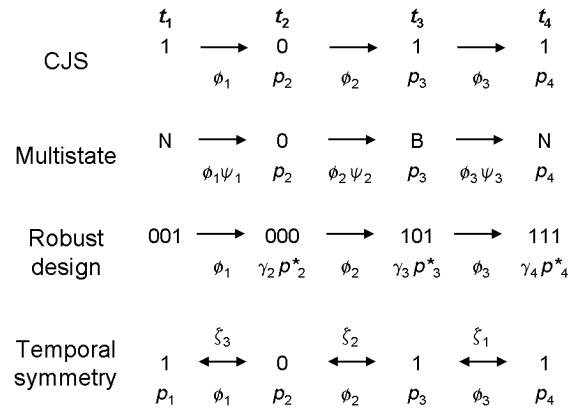
**Mark-recapture analyses based on live encounter data**

Mark-recapture analyses based on live encounter data improve upon return rates by separating the probability of apparent (or “local”) survival ( $\phi = S \times F$ ) from the probability of recapture ( $p = \gamma^* \times p^*$ ). Here, “live encounters” can include physical captures, resightings of colour-marked birds or some combination of the two. Mark-recapture statistics are a rapidly changing field and recent developments include new model selection procedures based on information theory (Burnham & Anderson 1998, Anderson & Burnham 2002), new statistical models (see below), and a new software package (Program MARK, White & Burnham 1999).

Modern mark-recapture analyses proceed in four general steps. First, capture histories are assembled for individual birds (Fig. 1). For example, years may be coded as: 1 = the bird was captured or resighted, or 0 = the bird was not detected. If inspection of capture histories reveals gaps where bird were not detected in intervening years (e.g., 1011), then the probability of recapture is < 1. Second, factors that will be included in the set of candidate models are selected *a priori*. In most demographic analyses, the factors will include sex, age-class and annual variation. Third, goodness-of-fit tests (GOF) are conducted to see whether the starting global model is a good fit to the data and whether corrections for overdispersion are necessary by calculation of a variance inflation factor ( $\hat{c}$ ). Last, reduced models with fewer numbers of parameters are fit to the data and the metrics of model selection (e.g., quasi-AICc values [QAICc] and Akaike weights) are used to identify the most parsimonious models.

At least 15 studies have applied mark-recapture statistics to live encounter data to estimate annual rates of  $\phi$  and  $p$  for open populations of waders (Table 1). All of these survival analyses have been based on standard Cormack-Jolly-Seber (CJS) models with either time- or age-dependence in the model structure. While clearly not an exhaustive sample of wader species, at least six general conclusions can be drawn from comparisons across these studies.

- 1)  $\hat{p}$  is < 1. More than 95% (23 of 24) of the overall estimates of the probability of recapture ( $\hat{p}$ ) were less than one (median  $\hat{p} = 0.67$ , range = 0.01 to 1.00). The sole exception was Johnson *et al.* (2001) who found that  $\hat{p} = 1$  for territorial Pacific Golden-Plovers *Pluvialis fulva* at a wintering site in the Hawaiian Islands. Nonetheless, the same authors found that  $\hat{p} = 0.70$  for nonterritorial birds at the same site.
- 2) Color ringing and other auxiliary marking schemes aid survival analyses by increasing the probability of recapture ( $\hat{p}$ ). Insley *et al.* (1997) and Piersma *et al.* (unpubl. MS) used metal rings only, and had to ring large samples of birds over a long periods of time to compensate for low recapture rates ( $\hat{p} < 0.2$ , Table 1). Twelve studies that based capture histories on resightings and captures of color ringed birds obtained higher probabilities of recapture ( $\hat{p} > 0.2$ , Table 1).
- 3)  $\hat{p}$  is affected by sex and year. Inspection of the best fit models in Table 1 reveals that sexual and annual variation in  $\hat{p}$  is commonplace. Thus, much of the variation in return rates may be due to variation in the probability of recapture. For example, sexual differences in return rates have been reported for Semipalmated Plovers *Charadrius semipalmatus* (male:  $rr = 0.601$ , female:  $rr = 0.410$ , Flynn



**Fig. 1.** Comparison of mark-recapture models for analysis of live encounter data for an example with four occasions ( $t_1$  to  $t_4$ ) and three intervals (arrows). Capture histories are coded as 1 = detected and 0 = not detected. In the multistate model, B = breeding, N = nonbreeding and 0 = not detected. Estimated parameters include the probabilities of apparent survival ( $\phi$ ), recapture ( $p$ ), changing states ( $\psi$ ), temporary emigration ( $\gamma$ ), detection ( $p^*$ ) and seniority ( $\zeta$ ).

*et al.* 1999) and Snowy Plovers *C. alexandrinus* (male:  $rr = 0.580$ , female:  $rr = 0.511$ , Paton & Edwards 1996). Badzinski (2000) and Paton (1994) used mark-recapture methods to analyse resighting data from the same populations and discovered sexual differences in  $\hat{p}$  but not  $\hat{\phi}$  (Table 1).

- 4)  $\hat{p}$  is affected by age-class. Four studies have estimated  $\hat{p}$  separately for birds banded as juveniles and adults (Table 1). Recapture rates ( $\hat{p}$ ) were lower among juveniles than adults in three breeding studies, but  $\hat{p}$  was higher among juvenile Western Sandpipers (*Calidris mauri*) than adults at a wintering site.  $p$  is usually viewed as a nuisance parameter but can have biological relevance because it includes site propensity ( $\gamma^*$ , see above). Age-specific variation in recapture rates of juvenile waders in the year after first ringing may indicate a lower probability of migration to breeding sites and a stronger propensity to remain at wintering sites.
- 5) Use of time-dependent models is widespread. A majority of wader studies have used time-dependent CJS models that allow  $\phi$  and  $p$  to vary with time and among groups (63.2%, 12 of 19 estimates, Table 1). This is a potential problem because time-dependent models are known to yield estimates of  $\hat{\phi}$  that are biased low if different individuals vary in their probability of capture. This is likely to be the case if returning individuals are pooled with transient or young birds that are not resighted after the sampling period in which they were ringed (Johnston *et al.* 1997). Several nonexclusive explanations can explain why birds might be captured on only one occasion: age-specific variation in survival or site fidelity, handling effects that lead to permanent emigration following first capture or the inclusion of transient individuals (Sandercock & Jaramillo 2002). Distinguishing among these alternatives is rarely feasible without auxiliary data.
- 6) Models that control for years since first capture give improved estimates of apparent survival. It is possible to control for birds captured on only one occasion with two types of mark-recapture models: age-structured models or transient models (Pradel *et al.* 1997). For example, a





**Table 1.** Results from 15 studies that have used mark-recapture statistics to estimate the probabilities of apparent survival ( $\hat{\phi}$ ) and recapture ( $\hat{p}$ ) for wader populations.

Species	Age <sup>a</sup>	Sex or group <sup>b</sup>	Range <sup>c</sup>	Type <sup>d</sup>	Best fit model <sup>e</sup>		Overall estimate <sup>f</sup>		No. yrs <sup>g</sup>	No. birds <sup>h</sup>	Source <sup>i</sup>
					$\phi$	$p$	$\hat{\phi}$	$\hat{p}$			
<i>Pluvialis apricaria</i>	A	MF	W	Time	con	con	0.73	<0.01	50	63387	1
<i>Pluvialis fulva</i>	A	T	W	Time	ac+terr	terr	0.85	1.00	10	112	2
		N					0.75	0.70		51	
<i>Charadrius alexandrinus nivosus</i>	J	MF	B	Time	con	con	0.39	0.21	4	171	3
	A	M		Time	t	sex	0.69	0.68		162	
		F					0.69	0.52		199	
<i>Charadrius alexandrinus alexandrinus</i>	J	MF	B	Age	2ac*t	con	0.09	0.41	5	1176	4
	A	M		Age	2ac*t	sex	0.63 <sup>j</sup>	0.84		432	
		F					0.63 <sup>j</sup>	0.74		469	
<i>Charadrius melodus</i>	J	MF	B	Age	2ac	con	0.32	0.26	9	143	5
	A			Time	t	t	0.74	0.44		204	
<i>Charadrius semipalmatus</i>	A	M	B	Age	2ac*t	sex	0.71	0.85	7	122	6
		F					0.71	0.64		134	
<i>Tringa totanus</i>	A	MF	W	Age	2ac*t	t	0.74 <sup>j</sup>	0.11	17	8153	7
<i>Numenius tahitiensis</i>	A	MF	W	Time	t	t	0.85	— <sup>k</sup>	3	189	8
<i>Limosa limosa</i>	A	MF	W	Time	area	area*t	0.90	— <sup>k</sup>	6	— <sup>k</sup>	9
<i>Calidris alpina</i>	A	MF	W	Age	2ac*t	con	0.74 <sup>j</sup>	0.71	4	1051	10
<i>Calidris canutus</i>	A	MF	W	Time	con	t	0.84	≤ 0.20	4	1603	11
<i>Calidris mauri</i>	A	MF	B	Time	con	con	0.57	0.80	4	236	12
<i>Calidris mauri</i>	J	M	W	Age	con	2ac	0.49	0.74	4	139	13
	A						0.45	0.54		117	
<i>Calidris maritima</i>	A	MF	W	Time	size	con	0.79	0.95	6	94	14
<i>Calidris pusilla</i>	A	M	B	Time	sex+t	t	0.61	0.77	8	237	15
		F					0.56	0.56		249	
<i>Calidris pusilla</i>	A	M	B	Time	sex	con	0.73	0.67	4	108	12
		F					0.59	0.67		122	

<sup>a</sup> Age: J = juveniles ≤ 1 year of age, A = adults ≥ 1 year of age.

<sup>b</sup> Sex or group: F = female, M = male, N = nonterritorial, T = territorial.

<sup>c</sup> Range: B = breeding site, W = wintering site.

<sup>d</sup> Type of mark-recapture model: Time = Cormack-Jolly-Seber (CJS) model with time-dependence only, Age = CJS model with two age-classes that separate apparent survival in the interval after first ringing from all subsequent intervals.

<sup>e</sup> Best fit model: model with the lowest value for AIC, AICc or QAICc, ignoring other models that were equally parsimonious ( $\Delta QAICc \leq 2$ ). Model factors include: + = main effect model without an interaction term, \* = factorial model with an interaction term, 2ac = two age-classes, ac = age as a group effect, area = region of ringing, con = constant, sex, size = bill size, t = time or annual variation, terr = territoriality as a group effect.

<sup>f</sup> Overall estimate: estimate from best fit model or average of annual estimates.

<sup>g</sup> No. yrs: duration of the study in years.

<sup>h</sup> No. birds: number of birds or bird years.

<sup>i</sup> Source: 1. T. Piersma *et al.*, unpubl. MS, 2. Johnson *et al.* 2001, 3. Paton 1994, 4. B.K. Sandercock *et al.*, unpubl. MS, 5. Larson *et al.* 2000, 6. Badzinski 2000, 7. Insley *et al.* 1997, 8. Marks & Redmond 1996, 9. Gill *et al.* 2001, 10. Warnock *et al.* 1997, 11. Brochard *et al.* 2002, 12. Sandercock *et al.* 2000b, 13. Fernández *et al.* 2003, 14. Summers *et al.* 2001, 15. Sandercock & Gratto-Trevor 1997.

<sup>j</sup> Estimate for adults in transitions subsequent to the second year after ringing ( $\phi^2$ ).

<sup>k</sup> Information not given by authors.

**Table 2.** Results from six wader studies that have used age-structured mark-recapture models to estimate apparent survival ( $\hat{\phi}$ ) separately for juveniles after first capture ( $\phi^1_{\text{juv}}$ ), adults after first capture ( $\phi^1_{\text{adt}}$ ), and adults in later transitions ( $\phi^2_{\text{adt}}$ ).

Species	Range <sup>a</sup>	Apparent survival <sup>b</sup>			Source <sup>c</sup>
		$\phi^1_{\text{juv}}$	$\phi^1_{\text{adt}}$	$\phi^2_{\text{adt}}$	
<i>Charadrius alexandrinus alexandrinus</i>	B	0.15	0.59	0.63	1
<i>Charadrius melodus</i>	B	0.32	–	0.77	2
<i>Charadrius semipalmatus</i>	B	–	0.62	0.77	3
<i>Tringa totanus</i>	W	0.43	0.67	0.74	4
<i>Calidris alpina</i>	W	0.33	0.53	0.74	5
<i>Calidris mauri</i>	W	0.45	–	0.49	6

<sup>a</sup> Range: B = breeding site, W = wintering site.

<sup>b</sup> juv = birds ringed in their natal year (fledglings at breeding sites, immature birds at wintering sites), adt = adults  $\geq 1$  year of age.

<sup>c</sup> Source: 1. Sandercock *et al.*, unpubl. MS, 2. Larson *et al.* 2000, 3. Badzinski 2000, 4. Insley *et al.* 1997, 5. Warnock *et al.* 1997, 6. Fernández *et al.* 2003.

model with two “age”-classes separates the transition immediately after first ringing for newly marked birds ( $\phi^1$ ) from subsequent transitions for previously ringed birds ( $\phi^2$ ). Six wader studies have employed two age-class models, and remarkably, all report similar results (Table 2, see also Sandercock & Jaramillo 2002). Apparent survival rates are consistently ranked: juveniles after first capture ( $\phi^1_{\text{juv}}$ ) < adults after first capture ( $\phi^1_{\text{adt}}$ ) < adults in later transitions ( $\phi^2_{\text{adt}}$ ). Moreover, the difference between  $\phi^1_{\text{adt}}$  and  $\phi^2_{\text{adt}}$  ranges from 4 to 21 percentage points in four species. Use of time-dependent models or treatment of age-class as a group effect effectively pools  $\phi^1_{\text{adt}}$  and  $\phi^2_{\text{adt}}$ , leading to underestimates of the apparent survival rates of adults.

### Considerations in estimating survival from live encounter data

One consideration in estimating apparent survival from live encounter data is that the standard Cormack-Jolly-Seber mark-recapture models require relatively long time series. For example, a four year dissertation project would yield four occasions and three annual estimates of apparent survival. However, if there is time-dependence in both  $\phi$  and  $p$ , then it is not possible to estimate  $\hat{\phi}$  for the last interval or  $\hat{p}$  for the last occasion (i.e.,  $\phi_3$  and  $p_4$  in Fig. 1). The product of apparent survival and the recapture rate for the last transition becomes an inestimable  $\beta$ -term that cannot be decomposed (i.e.,  $\phi_3 p_4$ ), and only two estimates of apparent survival would be possible.

A general problem of all models based on live encounter data is that they yield estimates of apparent and not true survival. The complement of apparent survival includes mortality and permanent emigration, and these two processes are usually confounded. In studies of migratory birds at breeding sites, permanent emigration due to natal or breeding dispersal is a likely feature of studies conducted on small-scale plots (Lambrechts *et al.* 1999). If study plots are set in a larger contiguous area of suitable habitat, even moderate rates of dispersal will remove breeding birds from the sampling area, thus underestimating true survival rates (Cilimburg *et al.* 2002). Estimates of dispersal distance can assist interpretation of variation in apparent survival rates (Sandercock *et al.* 2000b), but unfortunately, measurements of dispersal distance are also biased by the scale of study plots

(Jackson 1994, Koenig *et al.* 1996). Thus, apparent survival from breeding sites will be a good index of true survival only if rates of philopatry and breeding site-fidelity are high.

Fortunately for studies of waders, site fidelity is often high at both breeding and wintering areas. It is noteworthy that existing mark-recapture analyses of wader survival have been conducted for populations at both breeding and wintering sites (Table 1). To date, mark-recapture statistics have not been used to estimate apparent survival from captures of waders at stopover sites, although some species show strong site fidelity to staging areas used during migration (Smith & Houghton 1984, Harrington *et al.* 1988). For example, Pfister *et al.* (1998) reported annual return rates of 0.313–0.401 for Semipalmated Sandpipers *Calidris pusilla* returning to a stopover area in Massachusetts.

Ornithologists face different challenges when estimating survivorship from breeding and wintering populations. Sandercock & Jaramillo (2002) argued that estimates of apparent survival from wintering sites could be preferable to estimates from breeding sites for two reasons. First, fidelity to wintering sites is determined by ecological factors including knowledge of food and predator dispersion, whereas fidelity to breeding sites is determined by both ecological factors and genetic considerations related to mate selection. If site fidelity is stronger at wintering than breeding sites, then estimates of apparent survival from nonbreeding areas may be more reliable if disappearances reflect mortality and not permanent emigration. Second, if birds from different breeding sites intermingle at one wintering site then estimates of apparent survival from nonbreeding sites may be superior if they reflect conditions throughout the breeding range and not just a limited subset of breeding sites.

On the other hand, it may be more difficult to obtain a random sample of birds from populations at wintering sites. Differential migration is common in waders and wintering populations often show latitudinal clines in sex and age composition (Myers 1981, Nebel *et al.* 2002). Moreover, different sex and age-classes often utilize different habitats or roost sites within a single wintering site (Ruiz *et al.* 1989, Durell *et al.* 1993, Cresswell 1994). Sampling designs must be planned with caution to avoid systematic bias. Interpretations of apparent survival estimates based on live encounter data often benefit from prior knowledge of the ecological processes that are likely to affect wader population dynamics.



## Mark-recapture analyses based on dead recovery data

Mark-recapture models can also be used to estimate annual survival rates from ring recoveries of birds that are harvested or found dead. Dead recovery models differ from live encounter models in that ring recoveries are usually drawn from large geographic regions. As a consequence, estimates of survival ( $\hat{S}$ ) from dead recovery models are usually considered to be the true survival rate.  $\hat{S}$  can still be biased by permanent emigration if birds move to areas where they are less likely to be recovered, but this is less of a problem than analyses of live encounter data from small-scale study plots (Francis 1995a,b).

Capture histories for recovery models are coded with two columns per year, one for live encounters and one for dead recoveries, where 1 = detected and 0 = not detected (White & Burnham 1999). The recovery models of Brownie *et al.* (1985) estimate two parameters: true survival ( $S$ ) and recovery ( $f$ ), defined as the probability that a marked bird dies, is retrieved and reported. Brownie models include the early model of Haldane (1955) which assumes that survival does not vary with age, and that survival and recovery rates are constant across all years in the study period. Brownie models provide a robust and flexible framework for analysis of band recoveries, and can be used to examine age-specific variation in true survival and recovery rates if the ringing sample includes both young and adult birds (Francis 1995a). More recently, Catchpole *et al.* (1995) proposed an alternative recovery model that estimates survival ( $S$ ) and a different recovery rate ( $r$ ), defined as the probability that a dead marked bird is reported in a period between two releases. Where Brownie models emphasize recoveries from hunter-killed birds, Catchpole models deal with recoveries of all dead birds, regardless of the source of mortality.

Recovery models probably have limited utility for estimating survival rates for most wader populations. In North America, the proportion of rings recovered is low for non-harvested species of waders (median = 0.014,  $n = 28$  species, Wilcox 1959) and songbirds (mean = 0.004,  $n = 225$  species, Francis 1995b). Only two waders are legal game in North America: Wilson's Snipe *Gallinago delicata* and American Woodcock *Scolopax minor* (Tacha & Braun 1994, Kelley 2002). Recovery rates of American Woodcock are relatively low ( $f = 0.025$ – $0.045$ , Dwyer & Nichols 1982) compared to the proportion of rings recovered from waterfowl (median  $f = 0.135$ ,  $n = 35$  species, Franklin *et al.* 2002). Recovery models may have greater utility for wader populations in Europe for three reasons: better established ringing programs that have marked large samples of birds, a longer traditional harvest of waders and higher reporting rates. Haldane's method was applied to 23 species of European waders by Boyd (1962), and more recently, to Eurasian Curlew *Numenius arquata* (Bainbridge & Minton 1978) and Eurasian Woodcock *S. rusticola* (Hoodless & Coulson 1994). Modern recovery models have been applied to only four species of waders: Eurasian Oystercatcher ( $\hat{S} = 0.89$ , Atkinson *et al.* 2003), Northern Lapwing ( $\hat{S} = 0.71$ , Peach *et al.* 1994,  $\hat{S} = 0.83$ , Catchpole *et al.* 1999), Red Knot ( $\hat{S} = 0.79$ , Boyd & Piersma 2001a,  $\hat{S} = 0.88$ , Atkinson *et al.* 2003), and American Woodcock ( $\hat{S} = 0.35$ – $0.53$ , Dwyer & Nichols 1982).

## Models based on known fate data from radio-telemetry

Radio-telemetry can be used to obtain accurate data on the survival, movements and habitat use of waders (Krementz *et al.* 1994, Warnock & Takekawa 1996, Plissner *et al.* 2000, Sanzenbacher & Haig 2002). Survival analyses for radio-marked birds can be conducted with several different procedures (White & Garrott 1990, Williams *et al.* 2002). If survival rates are assumed to be constant over time, then daily survival rates ( $\hat{s}_i$ ) for a given interval ( $i$ ) can be estimated as:

$$\hat{s}_i = \frac{(x_i - d_i)}{x_i}$$

where  $x_i$  = the total number of transmitter days of exposure and  $d_i$  = the number of mortality events (Heisey & Fuller 1985). Period survival across multiple intervals is then:

$$\hat{S} = \prod \hat{s}_i^{L_i}$$

where  $L_i$  = the length of each interval. Time to failure models improve on this estimator because they allow survival rates to vary over time. These models include nonparametric Kaplan-Meier methods, proportional hazards models and continuous hazard functions (Tsai *et al.* 1999, Williams *et al.* 2002). If detection rates are  $< 1$ , mark-recapture models can also be applied to known fate telemetry data (Bunck & Pollock 1993).

One potential problem that may arise when using telemetry studies to estimate annual survival is that the battery life of small radios may be short relative to the life span of waders. Telemetry studies of adult plovers and sandpipers have reported few losses and therefore high daily survival rates ( $\hat{s}_i > 0.99$ , Table 3). American Woodcock are one of the few species of waders that have been well-studied with radio-telemetry methods. Telemetry studies of this species have reported high numbers of losses, resulting in lower daily survival rates (Table 3). Derleth & Sepik (1990) tested the assumption of constant survival and found that it was not valid for woodcock. Estimates of period survival for adult woodcock based on Kaplan-Meier methods include: 0.72 for a 77 day winter period (Pace 2000), 0.75 for a 45 day winter period (Krementz & Berdeen 1997), 0.79 for a 76 day breeding period (Longcore *et al.* 1996), and 0.92 for a 127 day summer-fall period (Derleth & Sepik 1990). Low estimates of period survival may indicate that radio-transmitters are impacting the survivorship of this species

## POTENTIAL APPLICATIONS OF NEW MARK-RECAPTURE MODELS

### Advanced models for live encounter data

A range of new mark-recapture models that are extensions of the CJS model are available for analysis of live encounter data. Empirical applications of these models are limited, so I describe four types of models and discuss their potential applications to wader populations.

1) Multistate models. Multistate models permit inclusion of



**Table 3.** Results from eight wader studies that have used known fate data based on radio-telemetry and the Heisey & Fuller (1985) method to estimate daily survival rates ( $\hat{S}_i$ ).

Species	Age <sup>a</sup>	Sex <sup>b</sup>	Range <sup>c</sup>	$\hat{S}_i$	Losses	Exp. <sup>d</sup>	No. birds	Period (days) <sup>e</sup>	Source <sup>f</sup>
<i>Charadrius montanus</i>	A	MF	B	1.0000	0	275	24	76	1
<i>Charadrius montanus</i>	A	MF	W	0.9996	1	2395	44	135	2
<i>Charadrius melodus</i>	A	MF	W	1.0000	0	2704	49	258	3
<i>Calidris mauri</i>	JA	MF	W	1.0000	0	–	99	–	4
<i>Scolopax minor</i>	J	M	B	0.9955	8	1792	49	127	5
	J	F		0.9976	4	1636	47		
	A	M		0.9992	1	1228	16		
	A	F		0.9990	1	1030	16		
<i>Scolopax minor</i>	J	M	W	0.9953	16	3371	114	62	6
	J	F		0.9920	20	2511	80		
	A	M		0.9939	4	653	23		
	A	F		0.9972	4	1404	39		
<i>Scolopax minor</i>	J	M	W	0.9944	1	178	7	45	7
	J	F		0.9878	2	164	6		
	A	M		0.9951	1	203	7		
	A	F		0.9916	1	119	5		
<i>Scolopax minor</i>	J	F	W	0.9953	26	5498	103	77	8
	A	F		0.9964	11	3070	57		

<sup>a</sup> Age: J = juveniles  $\leq 1$  year of age, A = adults  $\geq 1$  year of age.

<sup>b</sup> Sex: F = female, M = male.

<sup>c</sup> Range: B = breeding site, W = wintering site.

<sup>d</sup> Exp. = total days of exposure.

<sup>e</sup> Period = duration of study period.

<sup>f</sup> Source: 1. Miller & Knopf 1993, 2. Knopf & Rupert 1995, 3. Drake *et al.* 2001, 4. Warnock & Takekawa 1996, 5. Derleth & Sepik 1990, 6. Kremenz *et al.* 1994, 7. Kremenz & Berdeen 1997, 8. Pace 2000.

categorical data in the capture histories that are dynamic and change over the course of the animal's life span (Lebreton & Pradel 2002). Examples of strata that have been used in multistate analyses of other birds include breeding status (Cam *et al.* 1998, Sandercock *et al.* 2000a) and breeding colony (Spendelov *et al.* 1995, Lindberg *et al.* 1998). To include data on breeding status, an occasion in a multistate model could be coded as either B = breeding or N = nonbreeding, instead of 1 = resighted as in the CJS models (Fig. 1). One advantage of multistate models is that they yield estimates of apparent survival ( $S_B$  and  $S_N$ ) and recapture ( $p_B$  and  $p_N$ ) that are specific to each strata. The models also yield estimates of the transitional probabilities of changing strata between years, such as the probability that a breeder will become a nonbreeder ( $\psi_{B-N}$ ) and the probability that a nonbreeder will become a breeder ( $\psi_{N-B}$ ). The ability to separate survival and movement is possible under the assumption of temporal independence of the two events.

In waders, multistate models could be used in a variety of applications. They would be an improved method for examining survival rates at different winter roost sites and for determining rates of exchange among different roosts (Rehfishch *et al.* 1996, Pearce-Higgins 2001). A common observation among breeding waders is that return rates are lower among birds whose nesting attempts have failed (Gratto *et al.* 1985, Ryabitsev 1998, Flynn *et al.* 1999). Multistate models could be used to model the effects of nest failure on apparent survival.

- 2) Robust design models. Pollock's robust design models are similar to CJS models in that the capture histories are

coded with 1 = captured and 0 = not detected. They differ from CJS models in that the primary sampling periods (usually years) are subdivided into shorter secondary sampling periods (Fig. 1). Populations are assumed to be closed within secondary sampling periods and open between primary sampling periods (Kendall & Nichols 1995, Kendall *et al.* 1997), although robust design models perform well under most violations of the closure assumption (Kendall 1999). In a CJS model, the probability of capture ( $p$ ) is the product of the probability that the individual is in the population to be sampled ( $\gamma^*$ ) and the true probability of detection ( $p^*$ ).  $p^*$  is available from the closed population data in the secondary samples, where it is the sole parameter that defines the capture histories. In robust design models, closed population estimators are used to calculate  $\hat{p}_t^*$ , open population estimators are used to calculate  $\hat{p}_t$ , and the probability of site propensity is derived as:

$$\hat{\gamma}_t^* = \frac{\hat{p}_t}{\hat{p}_t^*}$$

One major advantage of robust design models is that  $\gamma^*$  and  $p^*$  are estimable for all occasions and it is always possible to estimate  $\phi$  for the last interval of a time series ( $\beta$ -terms are never present).

A second advantage of robust design models is that they permit estimation of site propensity ( $\gamma^*$ ) and temporary emigration ( $\gamma = 1 - \gamma^*$ , Kendall & Nichols 1995). In a breeding population, differences in  $\hat{\gamma}^*$  could reflect variation in the probability of breeding. If robust design



models are applied to a known age sample of birds, then  $\hat{\gamma}^*$  is effectively an age-specific estimate of the probability of breeding (Sedinger *et al.* 2001). For birds at a wintering or staging site, differences in  $\hat{\gamma}^*$  could reflect variation in migratory chronology that causes birds to be absent during sampling or may indicate failure to migrate. Alternatively, variation in  $\hat{\gamma}^*$  may reflect temporary dispersal after handling or incomplete sampling of territories at the perimeter of a study area.

Many waders are long-lived species where delayed maturation is likely. Unfortunately, our understanding of age-specific variation in breeding propensity is limited. Most of our current knowledge is confined to estimates of age of first breeding based on distributions of age at first capture (Evans & Pienkowski 1984, Gratto 1988, Thompson *et al.* 1994). Use of age at first capture assumes that detectability is complete, which is a problem because variation in age at first capture may reflect differences in  $p^*$  and not  $\gamma^*$ . Application of robust design models to wintering populations of waders would be an exciting new approach to address this issue. In many species of migratory waders, a subset of immature birds remain at wintering sites and forego northward migration and breeding during the boreal breeding season (McNeil *et al.* 1994, Summers *et al.* 1995, Marks & Redmond 1996). If robust design models were applied to known age birds at wintering sites, they could yield estimates of site propensity that could lead to a better understanding of the probability of northward migration, and possibly age-specific breeding propensity as well.

- 3) Temporal symmetry models. Capture histories for temporal symmetry models are coded in the same manner as CJS models. Temporal symmetry models differ from time-dependent CJS models in that the capture histories are simultaneously analysed with both forward and reverse-time modelling (Pradel 1996, Nichols & Hines 2002). Forward-time modelling yields the usual estimates of apparent survival ( $\phi$ ) and recapture rates ( $p$ ). Reverse-time modelling of the same capture histories from the last capture backwards yields a seniority probability ( $\zeta$ , sometimes denoted  $\gamma$ ), defined as the probability that an individual did not enter the population between the previous and current occasion. The parameters  $\phi$  and  $\zeta$  can then be combined to estimate two useful metrics of population dynamics,

the finite rate of population growth:

$$\hat{\lambda}_t = \frac{\hat{\phi}_t}{\hat{\zeta}_{t+1}}$$

and the per capita recruitment rate:

$$\hat{f}_t = \frac{\hat{\phi}_t (1 - \hat{\zeta}_{t+1})}{\hat{\zeta}_{t+1}}$$

The major advantage of temporal symmetry models is that they permit direct estimation of population growth rates without the need to either completely enumerate the population or to estimate all of the vital rates that would be needed to parameterize a population model based on a projection matrix. Sandercock & Beissinger (2002)

showed that field estimates of  $\hat{\lambda}$  from temporal symmetry models and matrix models are comparable for at least one bird population. Temporal symmetry models will be useful for any population study of waders, but may be of particular benefit for investigations of species of conservation concern. A potential drawback of temporal symmetry models is that they usually require long time series. Time-dependence in  $\hat{\phi}$  and  $\hat{p}$  leads to inestimable  $\beta$ -terms in both the first and last intervals of the study period and  $n$  occasions yields  $n - 3$  estimates of  $\hat{\lambda}$ .

- 4) Joint models for different types of data. Some of the most exciting new mark-recapture models combine multiple sources of information to obtain improved estimates of annual survival.
- a) Live encounter and known fate data. Powell *et al.* (2000) described a multistate model that combines live encounter data with known fate data from radio telemetry to estimate the probabilities of apparent survival ( $\phi$ ), movement off the study site ( $\psi$ ) and capture ( $p$ ). The authors give an empirical example with a forest thrush.
  - b) Live encounter and dead recovery data. Burnham (1993) developed a model that combines live encounter and dead recovery data to estimate the probabilities of true survival ( $S$ ), site fidelity ( $F$ ), reporting ( $r$ ) and capture ( $p$ ). Empirical applications of this model include waterfowl (Blums *et al.* 2002, Doherty *et al.* 2002) and one species of owl (Francis & Saurola 2002). This model could be applied to any ringing program for waders with recaptures and recoveries from the same site. For example, Boyd & Piersma (2001b) reported a minimum of 1233 recaptures and 812 recoveries from 87,786 Red Knots ringed in Britain.
  - c) Robust design and dead recovery data. Lindberg *et al.* (2001) developed a model that applies a robust design framework to live encounter and dead recovery data to estimate the probabilities of true survival ( $S$ ), site fidelity ( $F$ ), temporary emigration ( $\gamma$ ), capture ( $p$ ), recapture ( $c$ ) and recovery ( $f$ ). To date, this model has only been applied to a population of diving ducks.

### Estimation of survival on different time scales

The emphasis of this review has been annual survival, but the same set of mark-recapture models can be used to estimate survival on different time scales. Capture histories coded on a daily basis have been used to look at probability of departure from a stopover site in sandpipers (Pollock *et al.* 1990, Holmgren *et al.* 1993) and other migratory birds (Kaiser 1995, 1999, Frederiksen *et al.* 2001). Temporal symmetry models based on daily capture histories have proven to be a powerful tool for estimating stopover duration of migratory songbirds (Schaub & Jenni 2001, Schaub *et al.* 2001).

Capture histories for live encounter data that are coded on weekly or monthly time scales and radio-telemetry are both well-suited for estimation of seasonal survival. Dwyer *et al.* (1988) used CJS models to calculate seasonal estimates of apparent survival for breeding woodcock. Combined data can also be used to decompose annual survival rates into their seasonal components. For example, Derleth & Sepik (1990) and Longcore *et al.* (1996) combined seasonal estimates of



survival from radio-telemetry with annual estimates of survival from dead recoveries to calculate seasonal variation in the survivorship of woodcock. In a similar approach, Sillett & Holmes (2002) used live encounter data to estimate monthly survival rates for a warbler at two locations: a breeding site in the United States and a wintering site in Jamaica. The authors combined estimates of survival for the two stationary periods with estimates of annual survival and were able to estimate mortality rates during migration. Comparable estimates of seasonal survival could be obtained for waders with similar methods.

## RECOMMENDATIONS FOR FUTURE STUDIES

Ornithologists studying wader populations have not made best possible use of the statistical tools that are available for estimation of survival and other demographic rates. In most cases, population data have been analysed with relatively simple methods. Live encounter data are often reported as return rates. Where mark-recapture methods have been applied, the starting global model has usually been time-dependent CJS models, which yield biased estimates if the sample contains transient individuals that are not resighted after ringing. Similarly, dead recovery data have usually been analysed with the early model of Haldane (1955), and known fate data from radio-telemetry with the methods of Heisey & Fuller (1985). From this review, I offer eight recommendations that apply to retrospective analyses of existing data and to the development of future projects.

- 1) Estimation of annual survival from maximum longevity, age ratios and life tables should be avoided because the assumptions of these methods are unlikely to be met in field studies.
- 2) Population studies that collect live encounter data should use mark-recapture models wherever possible. Comparisons of 15 wader studies that used mark-recapture statistics revealed that the probability of recapture ( $\hat{p}$ ) is consistently  $< 1$  and is often affected by sex or annual conditions (Table 1). Thus, apparent survival values derived from mark-recapture modeling are better estimates of true survival than return rates.
- 3) Color ringing schemes should be used wherever resightings are feasible because they increase the probability of recapture ( $\hat{p}$ ). Mark-recapture analyses require much larger samples of ringed birds and longer study periods if only metal rings are used (Table 1).
- 4) Age-structured models with two age-classes are a better starting global model for analysis of live encounter data than time-dependent model. To date, every wader study that has used age models has found that apparent survival rates are low in the interval after first ringing and then higher in later intervals, even among birds ringed as adults (Table 2).
- 5) Stochastic recovery models should be more widely used for analysis of dead recovery data. In particular, it would be valuable to reexamine the recovery data available for European waders and to update the survival estimates published forty years ago by Boyd (1962). Survival analyses would be assisted if reporting rates could be increased, possibly by public outreach programs that encourage hunters and naturalists to report rings recovered from dead birds.
- 6) Publication of the underlying capture histories or recov-

ery matrix is desirable because the data can then be reanalysed either as a teaching tool or to explore alternative models not considered by the original authors. Paton (1994) and Badzinski (2000) are two authors who have provided this information.

- 7) As radio technology continues to improve, radio-telemetry will play an increasing role in estimation of survival rates for waders. Days of exposure and number of mortality events should always be reported, even if the research focus is habitat selection or another topic. Time to failure models have received limited use and should be applied whenever possible. Telemetry studies should also examine the effects of radios and attachment methods on wader survival whenever it is feasible to do so.
- 8) Ornithologists working with waders are encouraged to take advantage of new mark-recapture models (Fig. 1). Multistate models require considerable amounts of data to develop but offer robust estimates of movement rates for parameterization of metapopulation models. Robust design models require some additional sampling but differ from CJS models mainly in the format of the capture histories. Applying robust design models to wintering populations could yield the first estimates of age-specific breeding propensity in waders. Temporal symmetry models could be used to estimate population growth rates or stopover duration of migratory waders. Combined recapture-recovery models require data that will be available for only a few wader populations but have great potential because they offer unbiased estimates of breeding site fidelity.

In conclusion, modern quantitative methods offer better estimates of survival and other demographic rates for wader populations. A better understanding of wader demography will benefit basic research in evolutionary ecology and the applied goals of conservation biology.

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